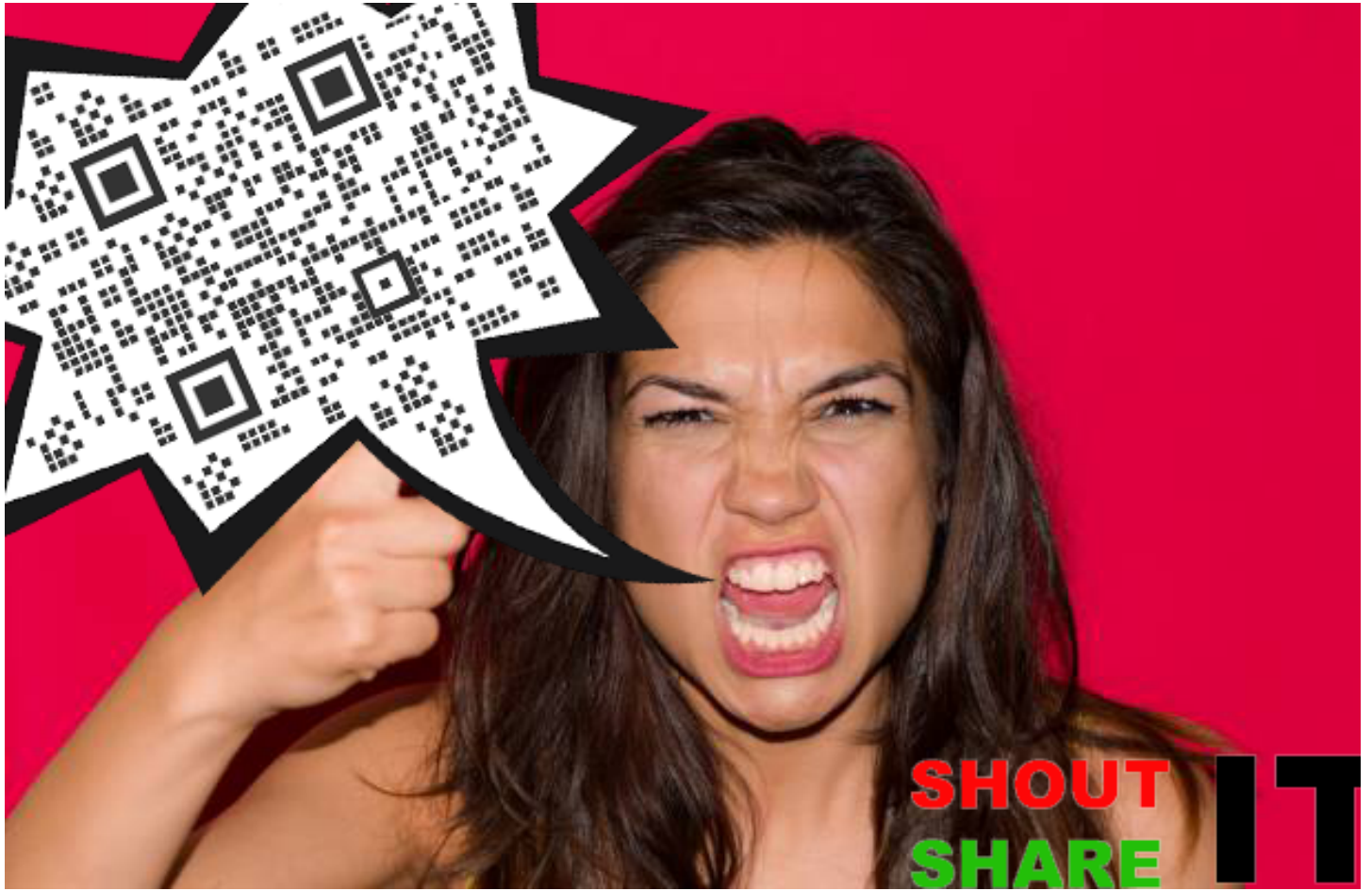




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Vol. 68

No. 288

NORTH AMERICAN PARACRINOIDEA:
(ORDOVICIAN:PARACRINOZOA, NEW,
ECHINODERMATA)

By

RONALD L. PARSLEY

AND

LEIGH W. MINTZ

1975

Paleontological Research Institution
Ithaca, New York 14850 U. S. A.

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NORTH AMERICAN PARACRINOIDEA: (ORDOVICIAN:PARACRINOZOA, NEW, ECHINODERMATA)

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ABSTRACT

Paracrinoidea is a class of primitive, approximately bilaterally symmetrical "pelmatozoic" Echinodermata which is essentially limited to the Middle Ordovician of North America. Their affinities are in part crinozoan — uniserial, pinnulated arms, thecal plates growing by overlaying; and part blastozoan — blastoid-like column, cystoid-like theca, arms probably without water vascular system. Paracrinoids do not fit into either of the accepted "pelmatozoan" subphyla so the subphylum Paracrinozoa, new, is proposed. Features unique to paracrinoids are peristome-gonopore axis of bilateral symmetry, internally opening transutural slits and proliferation of thecal plates on the right lateral part of the theca. Paracrinoids with transutural slits, the Order Comarocystitida, new, include in the family Comarocystitidae with the genera *Comarocystites* (*C. tribrachius*, n. sp.) and *Sinclairiocyctis*, and the family Amygdalocystitidae with the genera *Amygdalocystites*=*Ottawacystis*, *Oklahomacystis*, new and *Achradocystites*. Paracrinoids without transutural slits, the order Platycystitida, new, include in the family Comarocystitidae with the genera *Comarocystites* and *Canadocystis*=*Sigmacyctis* (*C. tennesseensis*, n. sp.), and the family Malocystitidae with the genera *Malocystites* and *Wellerocystis*.

Paracrinoids are not ancestral to or descended from any known echinoderms. They apparently lived in shallow, fairly active marine environments.

INTRODUCTION

Paracrinoids are generally uncommon fossils and are limited in time and space. They are restricted to North America, east of the 100th meridian, and are rarely found in Scotland and Estonia. Paracrinoids range exclusively in the Middle Ordovician (Chazy to Trentonian), except for the specimens from Scotland which are Upper Ordovician (Ashgillian) in age (Paul, 1965, pp. 474-477).

Paracrinoids are somewhat diverse in morphology but do form a distinct phylogenetic group. In the *Treatise on Invertebrate Paleontology*, Ubahgs (1968, pp. 51, 53-56), following Fell (1965, pp. 3, 13, and 14), placed the paracrinoids in the subphylum Crinozoa (Matsumoto, 1929) which also included the "pelmatozoan" classes Eocrinoidea, Cystoidea, Blastoidea, Parablastoidea, Edrioblastoidea, Lepidocystoidea, and Crinoidea. Ubahgs (*op. cit.*, p. 53), in part, characterized the Crinozoa as follows:

— echinoderms which are 1) affected in varying degree by radial (generally pentamerous symmetry; 2) typically characterized by a globoid, pyraform, or cup-shaped body (theca) enclosing the visceral mass or the main part of it, and 3) provided with food-gathering appendages which are either simple exothecal projections (brachioles of noncrinoid Crinozoa) or evaginations of the body wall carrying extensions of the coeloms and various systems of organs with them (arms of crinoids).

Paracrinoids fit this subphylum definition except for their lack of radial symmetry. They are clearly bilaterally symmetrical.

Sprinkle (1973, pp. 12-58) convincingly removed from the Crinozoa those "pelmatozoans" with simple exothecal projections (brachioles) and placed them in a new subphylum Blastozoa. Blastozoans include all of the classes listed above except for the Crinoidea, Paracrinioidea and possibly the diploporid cystoids. Brachioles are typically biserial and apparently without an open water vascular system traversing their length. Sprinkle (*op. cit.*, p. 19) pointed out that brachioles are remarkably conservative structures and are present and distinct in all blastozoan classes, some as early as the early Cambrian.

Morphologically, paracrinoids resemble crinoids in that they bear exothecal or epithecal uniserial arms with a single uniserial pinnule (with biserial covering plates over the food groove) extending from each arm plate or segment. There is, however, no evidence that the water vascular system traversed the length of the arms and pinnules, hence no respiratory-feeding tube feet on them, and, therefore, they apparently functioned as brachioles which characterize the Blastozoa.

Blastozoans are also characterized by thecal plates that grow primarily peripherally with most of the secondary thickening occurring on the interior surface of the plate (holoperipheral growth, Sprinkle, 1973, p. 45). This mode of growth contrasts with crinozoans, including paracrinoids, where the periphery (lateral margins) and the outside surface of the plate increase in size by addition of contiguous layers (overlaying primary plate growth, Sprinkle, 1973, pp. 45-46). Addition of calcite on the interior surface generally does not occur in crinoids but is observed in paracrinoids.

Many blastozoans have some kind of externally opening sutural pore arrangement manifest in structures such as epispires, pectinirhombs, or hydrospires. These structures were apparently all respira-

tory in function and some of them may have included parts of the water vascular system. Crinozoans in the restricted sense usually lack such structures in the theca. There are several exceptions in the crinoids, e.g., *Porocrinus* (Kesling and Paul, 1968), but they are not uncommon in paracrinoids. In paracrinoids internally opening sutural pores or slits are present (order Comarocystida, new) which are closed to the exterior by a thin "epistereom" or epithecal layer of calcite. Presumably these structures are also respiratory with gaseous exchange having occurred *via* the stromal strands through the epistereom. These structures are not folds in the stereom as commonly seen in blastozoans and some crinoidea, but instead are passageways or excavations in the plates. In paracrinoid genera with sutural slits, some secondary filling of the slits occurs near the center of the plates. Paracrinioidea, therefore, show similarities in plate structure to both the Blastozoa and crinoid Crinozoa.

Paracrinoid plate arrangement and general thecal morphology are generally cystoid-like. Some genera have a fairly well-fixed plate arrangement (Platycystitidae, new), others are variously polyplated. The right lateral part of the theca usually is composed of more numerous plates than the rest of the theca and in many genera this area is protuberant.

The hydropore and gonopore are located on the posterior lip of the peristome. The principal plane (anterior-posterior) of symmetry, the G plane, passes through the gonopore and the middle of the peristome. This plane of echinoderm symmetry is unique to the paracrinoids.

The column is blastoid-like, having short columnals which are pierced by a lumen (up to one-third the diameter of the column in width) which traverses the length of the column. The articulating surfaces are crenulate which assures a strong and fairly rigid stem.

From the brief introduction above, it is clear that the Paracrinioidea do not easily fit in either the Blastozoa or the Crinozoa. They are distinct, and at the expense of creating another higher taxon for such a small group, the subphylum Paracrinozoa, new is herein proposed.

The distinctness of the paracrinoids was first recognized by Jaekel, 1900, as being a group (Eustelea) different from other cystoids as then recognized. Subsequently, Foerste (1916), Jaekel

(1918), and others reaffirmed the distinct nature of this group, usually on an ordinal level (see below). Regnéll (1945) established the class Paracrinoidea and diagnosed it as follows:

A class of Pelmatozoa, the plate-system of which is not affected by polymeric symmetry and shows no differentiation into a calycinal and terminal portion; the exothecal subvective skeletal appendages are developed as uniserial brachia (free or recumbent) bearing uniserial pinnulae; a sub-epithecal pore-system is present in typical forms.

Regnéll (1945, pp. 37-38) pointed out that these forms "have for a long time been the subject of different opinions with regard to their systematic position." Even from his brief diagnosis the distinctness of the group is clear. Some doubt was cast on the validity of uniserial arms as a taxobasis by the possibility of biserial arms in *Achradocystites* (Hecker, 1958) by Regnéll (1960), p. 73).¹ He suggested that perhaps the "salient point in the morphology of the paracrinoids is the peculiar nature of the pore-system rather than the uniseriality of the exothecal subvective appendages." Regnéll (*op. cit.*) in part concluded that genera assigned to the Paracrinoidea cannot be definitely stated to have genetical affinity. "The group may be artificial."

Kesling (1968), in the *Treatise on Invertebrate Paleontology*, followed Jaekel (1918) in his classification. He included some genera not herein considered to be paracrinoids but implicitly considered the class as a natural grouping.

Sprinkle (1973, p. 184) published a more detailed diagnosis of the class and is in general agreement with that herein.

Regnéll (1945, pp. 37-40) noted, as did Foerste (1916, p. 71), that genera such as *Comarocystites* and its allies were not "normal" cystoids because they have uniserial instead of biserial arms. The arms are similar to those of most crinoids, but the theca does not consist of the same recognizable plate series (basals through orals), nor is there a well-differentiated tegmen developed. Where present, *e.g.*, *Sinclairocystis*, *Comarocystites*, the sub-epistereom sutural pore system, though similar to that of some rhombiferans, is unique to the paracrinoids.

¹The arm attachment bases are suggestive of a biserial arrangement. The arms themselves have not been observed. The oral area and arm attachment bases are similar to the non-pored genus *Columbocystis*, Bassler, a genus usually included in the eocrinoids, but placed in the paracrinoids by Sprinkle (1973, p. 138). *Columbocystis* herein is not included in the paracrinoids.

Comarocystites, in Regnéll's original discussion, was considered more or less typical of this class. However, it will be shown here that, to the contrary, it is atypical compared to other paracrinoid genera. Regnéll (*op. cit.*) also included *Amygdalocystites*, *Canadocystis*, *Wellerocystis*, and *Platycystites* in the class. *Achradocystites* and *Malocystites* were doubtfully placed here by him because of their uncertain affinities.

The original description and figures of *Achradocystites* (Volborth, 1870, pp. 9-11, figs. 3-10), and subsequent work by Hecker (Gekker, 1958, pp. 145-162, pls. 1-3), indicate that the genus is probably a paracrinoid. Volborth's drawings and Hecker's plates of the sutural pore structure of the thecal plates indicate that it is similar to that of *Sinclairocystis*. The column seems similar to that of *Comarocystites*. This genus is still poorly known because of the limited material and its poor state of preservation.

Malocystites is also a paracrinoid. Typically the recumbent, uniserial pinnules are missing from specimens of this genus and only the scars on the slightly raised, underlying calluses give evidence of their presence. The pinnule pattern on the theca resembles that of the recumbent arms on *Wellerocystis*. Other thecal characteristics are also similar in these two genera.

Subsequent to Regnéll (1945), other genera have been added to this class by several authors. Most of these genera are incorrectly placed in this class or are synonymous with other paracrinoid genera. Bassler (1950, pp. 274, 276) placed three new genera in this class.

Billingsocystis Bassler, 1950, from the ?Curdsville Limestone of Woodford County, Kentucky, may be the same as *Amygdalocystites radiatus*, as evidenced by unweathered plates and nature of proximal column. Kesling (1967) placed this genus in the Comarocystitidae which seems incorrect because of the completely dissimilar thecal plates and the lack of sutural pores in *Billingsocystis*.

Schuchertocystis Bassler, 1950, from the Benbolt Formation, Washburn, Tennessee, was put in the Comarocystitidae by Bassler, and Kesling (1967) concurred. Examination indicates that it does not belong in either the family or the class Paracrinoidea. Its affinities appear to be with some of the primitive rhombiferan cystoids.

The apical system, anal area, and sutural pores, have little in common with paracrinoids. The structure of the exothecal arms is unknown.

Sinclairocystis Bassler, 1950, was also placed in the Comarocystitidae by its author. Kesling (1968) assigned it to the Amygdalocystitidae. This assignment probably is not correct. While this genus is an undoubted paracrinoid, it is most closely related to *Comarocystites*. The externally concave thecal plates and the greatly expanded sub-epistereom sutural pores in these two genera are remarkably alike. *Sinclairocystis* exhibits other typical paracrinoid traits in the ambulacra, column attachment and hydro-gonopores.

Wilson (1946) did not recognize the class Paracrinoidea, perhaps because her publication date was so close to that of Regnéll (1945). She did, however, name a "cystoid," *Ottawacystis*, which is a true paracrinoid. The specimen of this monotypic genus has well-preserved arm pinnules but its thecal plates are worn. Examination of the specimen has led the authors to follow Kesling (1968) and place it in synonymy with *Amygdalocystites*, where it had been assigned originally by Billings (1858).

Sprinkle (1973, pp. 138, 186) added to the Paracrinoidea the genera *Columbocystis*, *Springerocystis*, and *Foerstecystis* (from the Benbolt Formation and all described by Bassler, 1950), which he removed from the Eocrinoidea. Tentatively he also suggested (*op. cit.*, p. 186) that *Ulrichocystis*, *Paleocystites*, and *Allocystites* may also be paracrinoids.

These genera are not included in the Paracrinoidea by the authors. The ambulacra are unknown and many of their thecal characteristics do not fit in what we consider to be paracrinoidal features.

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MORPHOLOGY

Arms and related structures.—The primary unifying trait of this class is the possession of transverse, uniserial and pinnulate arms which may be exothecal or epithecal. They vary in number from the inferred primary transverse pair, *e.g.*, *Sinclairocystis*, up to six or more branches from the primary pair, *e.g.*, *Wellerocystis*, *Malocystites*. In *Comarocystites* the primary arms bifurcate at one or both ends of the primary (epithecal) transverse food groove. Either three or four exothecal arms result. Three epithecal arms occur in *Oklahomacystis tribrachiatus*, new and, as is typical in this class and some of the three-armed cystoids, it is generally the left arm that bifurcates. In *Comarocystites* the left arm always bifurcates. Some genera, such as *Sinclairocystis*, show evidence that the epithecal arms may have been exothecal in the early juvenile stage.

Foerste (1916, p. 73) noted in reference to *Comarocystites* that the arms are homologues of "the lateral arms of the five-rayed cystids, there being no arm corresponding to the anterior arm of other cystids." The homology is, in part, valid because the multiple arms, epi- or exo-thecal, are bifurcations of the primary transverse pair, which occur in epithecal, two-armed genera.²

Each epithecal paracrinoid arm has two distinct sides or lateral faces: a straight, vertical side with undifferentiated surface interrupted only by plate sutures, and the opposite face where there is an incised, rounded food groove which is the main conduit to the oral opening. This groove may open laterally or, in some, almost abthecally. In the latter case, the side opposite the groove is relatively featureless. Perhaps the facing of the groove is simply indicative of arm rotation on the theca. On forms with epithecal arms, whether two-armed or multi-branched, the main food groove occurs on mutually opposite sides of the arms, with the groove on the right arm and its branches always posterior and on the left arm and its branches always anterior, e.g., *Amygdalocystites*, *Sinclairocystis*, *Platycystites*, and *Wellerocystis*. On the same side, a short groove extends from this main groove to the dimpled or slightly concave pinnule seat on the top (abthecal face) of each uniserial arm plate.

A uniserial pinnule extends from the upper surface of each uniserial arm plate. Pinnule lengths vary, but the few specimens on which such structures are still preserved indicate they probably

² It is possible that the "cystidean" transverse pair is indeed more primitive than the primordial, triradial configuration of some authors. The anterior arm in the triradial condition is a solution to the problem of gaining more subventive area, hence greater efficiency, relative to the surface area and volume of the theca. Arms extending posteriorly from the peristome would be stopped by the internal and external apparatus comprising the hydropore (water vascular system), gonopore and probably, in primitive forms, the anus. It would then follow that in the derived triradial condition the arms would adapt equal inter-ray angles for more efficient feeding. Bifurcation of the primary pair would permit the posterior ambulacrum from each arm to surround the hydropore-gonopore-sometimes-anal area (in adjusting to equal inter-ray spacing) but not extend through it. This would result in the typical bipentaradial appearance of many echinoderms. This does not suggest that the water vascular system is necessarily involved (Heider, 1912) or that this process could not have occurred a number of times (Ubaghs, 1968, p. 49). We do suggest, however, that a transverse bilateral symmetry is one of the earliest observable forms of symmetry in the primitive echinodermata. In some cystoid-like forms the anterior arm is a proximal anterior splitting of the left primary arm, viz., *Oklahomacystis triradiatus* (Bassler) among paracrinoids and *Triamara cutleri* Tillman among cystoids.

never exceeded the height of the theca in length. The adoral or primary pinnule on each arm is, however, considerably longer than the others, apparently up to one and one-half times as long, and typically has a somewhat thicker diameter. The primary arm ossicle is also correspondingly enlarged. The other pinnules are all of nearly the same diameter at the base. They sharply taper at the distal end. The length of the pinnules becomes progressively shorter away from the peristome.

Articulation between the bases of the pinnules and the arms appears to be rigid, but the other pinnular sutures suggest that moderate movement was possible. In species with epithecal arms, the food grooves are on the adoral sides of the antero-posteriorly, slightly compressed pinnules. In genera with exothecal arms, such as *Comarocystites*, the food grooves on the arms and pinnules are present but poorly known.

The structure of the covering plates over the food grooves on the arms and pinnules is unusual in this class. Unfortunately, they are known in only a few genera, *i.e.*, *Amygdalocystites* and *Platycystites*. The main food groove is lateral and covered by biserial covering plates. The lower (proximal) plates are (generally) approximately twice as long as those in the upper (distal) series. The width of two proximal covering plates roughly equals the width of three distal covering plates. Both series form a tightly sutured, shallowly pitched and generally non-erectile arch. At the juncture of the main groove with each of the pinnular grooves, the distal series becomes a double, alternating series, extending the length of the pinnule to the pinnule base. Presumably this loosely sutured series was erectile on the pinnules. The mechanism by which the distal series passes smoothly from a single to a double series is enigmatic.³

The arms are internally transversed by a lumen which, in contrast with the Crinoidea, does not extend into the pinnules. In some of the genera with epithecal arms, *e.g.*, *Sinclairocystis*, *Platycystites*, and *Wellerocystis*, the proximal part of the lumen is enlarged and expands toward the theca so that the cavity is floored by the under-

³ Possibly in the early evolution of the paracrinoids the arms lacked pinnules. The extension of the covering plates onto the concomitantly emerging pinnules resulted in the incorporation of the distal covering plate series on the sides of the pinnule groove. This would allow the serial repetition of this single series up both sides of the pinnule groove and result in a biserial arrangement.

arm thecal callus. Slight enlargement also occurs along the adthecal parts of the arm ossicle sutures of the proximal part of the arm. Distally, the lumens in epithecal arms are usually reduced in size, except in *Wellerocystis*, but may continue to narrowly extend from the ventral axial part of the ossicle to the thecal callus. Connection of these coelomic canals with the interior of the theca occurs at the base of the primary ossicle of each transverse arm. The lack of unaltered specimens, mostly because of recrystallization, makes accurate observations on coelomic canal connections extremely difficult.

Theca. — Paracrinoids vary considerably among genera in thecal morphology, e.g., thecal profile and cross-sectional outline, number and arrangement of plates, prosopon, nature of underarm calluses (in genera with epithecal arms) and the presence or absence of thecal pores. These characteristics are summarized in Table 1.

Variation in thecal shape is considerable. Profiles vary from rounded to amygdaloidal in two-armed epithecal forms, such as *Amygdalocystites* and *Platycystites*, to subrounded to rounded in forms with branched epithecal arms or pinnules, such as *Wellerocystis* and *Malocystites*, to ovoid-fusiform in exothecal-armed genera, such as *Comarocystites*. In cross-section, paracrinoid thecae are typically circular to subcircular, except in the two-armed epithecal genera which are typically evenly elliptical (biconvex) and may be considerably compressed.

Recognizable plates series, as found in crinoids, blastoids and some cystoids, are generally not present in the paracrinoids, except in the Platycystitidae, new. "Basals" and "orals" can be identified by their juxtaposition to the column and peristome, respectively. Basals are three in number and there are usually four peristomals.

Prosopon and the nature of the external plate surface is sometimes diagnostic. In *Comarocystites* and *Sinclairocystis* the external faces of the thecal plates are concave. Well-developed radiating prosoponal ridges are present on *Amygdalocystites*. Some genera are relatively smooth except for a fine to coarse pustulose prosopon, e.g., *Malocystites*, *Canadocystis*, and *Sinclairocystis*.

Two types of thecal plates occur in paracrinoids: thick-plated forms with elongated transutural pores and thinner plated forms in which such pores are completely lacking (Sprinkle, 1973, p. 184). With the possible exception of the poorly known species *Amygdalo-*

TABLE 1. CHARACTERISTICS OF PARACHINOD GENERA*

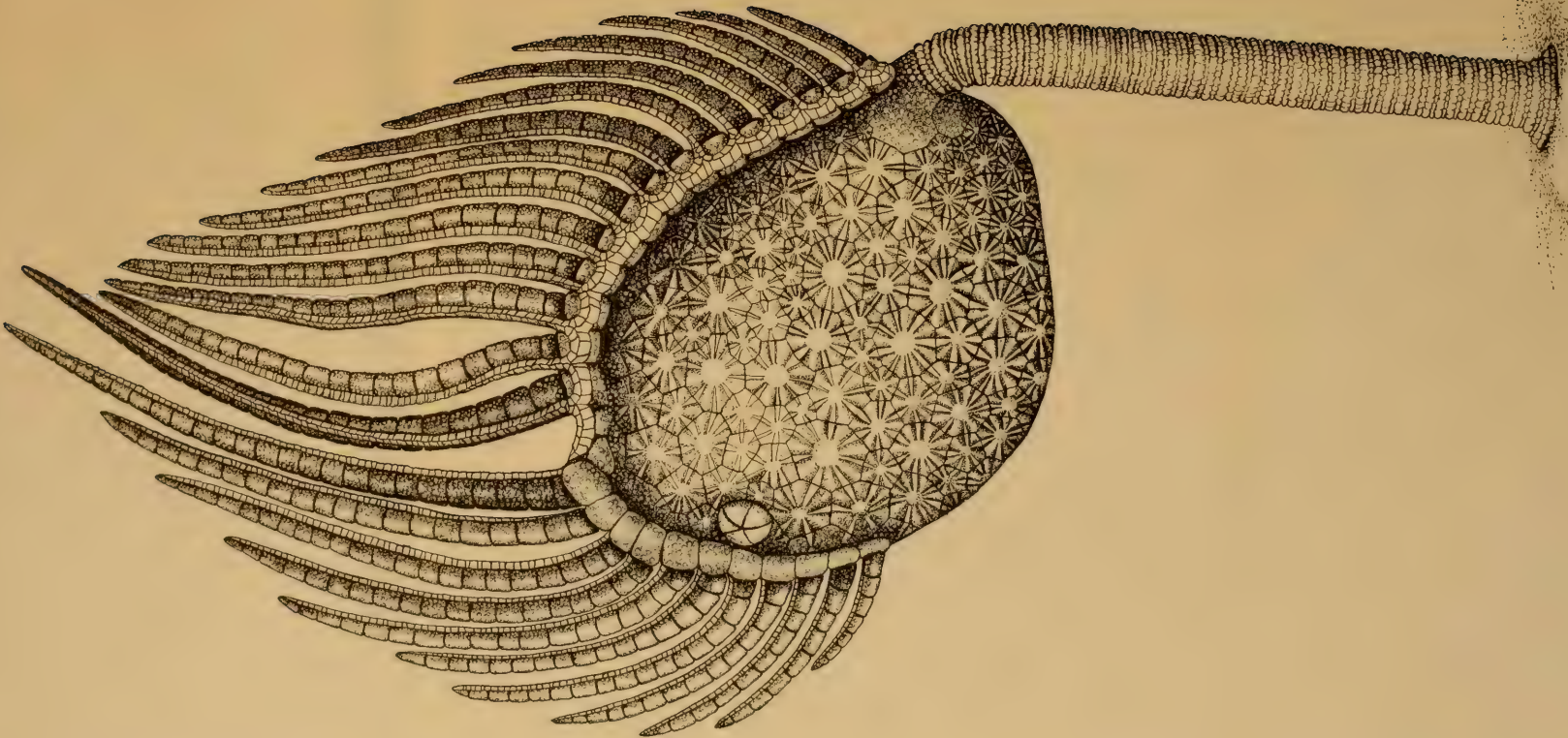
Genera	Shape of Theca	No. of Plates	Pore System	Plate Surface- Proson	Arms	No. of Arms- Branching	Age
<u>Comarocystites</u>	Ovate-fusiform	ca. 65-225	Numerous transverse pores across each plate facet	Plates externally concave	Exothecal	3 or 4, left primary arm always branched	Blackriverian-Trentonian ?Ashgillian
<u>Sinclairocystis</u>	Ovate-globular	27-52 average 37	Numerous transverse pores across each plate facet	Plates externally concave-pustulose	Epithcal	2, right arm sometimes curves onto posterior face	Blackriverian
<u>Amygdalocystites</u>	Amygdaloidal,	ca. 50-180	Usually 2 transverse pores across each plate facet	Radiating ridges on thecal plates	Epithcal	2, transversely arranged	Trentonian
<u>Oklahomaocystis</u>	Ovate-biconvex to globular	30 - ca. 95	Usually 2 transverse pores across each plate facet	Plates pustulose; trigonal pyramids arranged in rosettes	Epithcal Impressed	3, left arm branched, one branch of which on anterior face	Blackriverian
<u>Achradocystites</u>	Ovate-globular	ca. 1000-1200	Usually 1 transverse pore across each plate facet	Pustulose, pustules tunneled by transverse pores	Exothecal	3, left primary arm bifurcates at peristome so can be regarded as an independent third arm	Zones DII and DIII uppermost Middle Ordovician
<u>Platycystites</u>	Amygdaloidal biconvex	27-29 Identifiable maximum with intercalates, ca. 47	None	Finely pustulose	Epithcal	2, transversely arranged	Blackriverian
<u>Canadocystis</u>	Globular to subfusiform	22 Identifiable maximum with intercalates; 40 +	None	Smooth	Epithcal with tendency for arm tips to be exothecal	2, sigmoidally arranged	Chazyan-Blackriverian
<u>Malocystites</u>	Globular	33-58	None	Pustulose proson	Epithcal very short, with 8 to 10 recumbent pinnales	2, sigmoidally arranged	Chazyan
<u>Welleroocystis</u>	Ovate to subpyriform	30-44	None	Smooth	Epithcal with lumens extending the length of the arm	4 or 6, both primary arms branched	Blackriverian

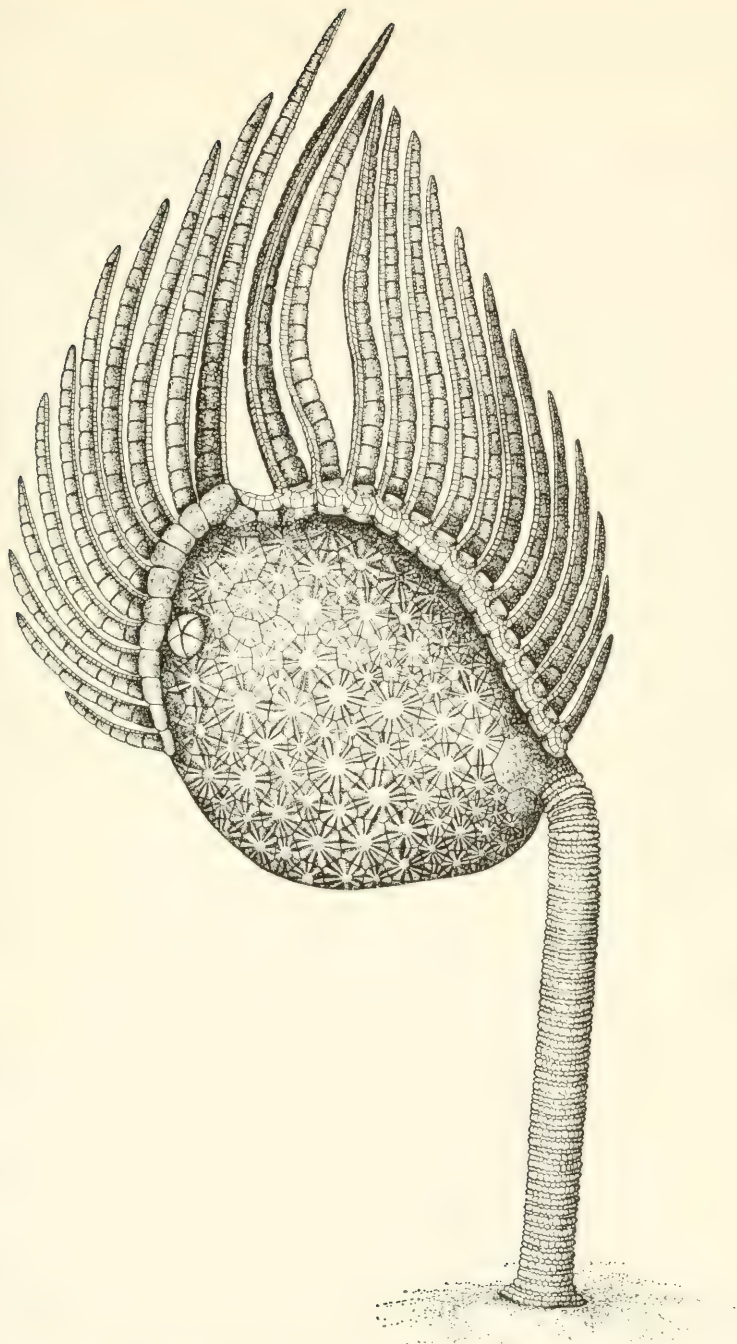
cystites radiatus Billings, no sutural pores (seen in unweathered specimens of this class) open to the exterior. All are covered by a thin "epistereom."⁴ The presence or absence of sutural pores can be used for ordinal classification in this class. This is considered by the authors as a sounder phylogenetic taxobasis than the free or attached nature of the arms used by Jaekel and modified by Kesling (1968) in the *Treatise on Invertebrate Paleontology*. Detailed morphological descriptions of the pore structures are found in the appropriate generic descriptions, i.e., *Amygdalocystites*, *Comarocystites*, *Sinclairocystis*, and *Oklahomacystis*.

Transutural pores are assumed to be part of the water vascular system (just as are port rhombs) and, as such, indicate that the system was large (in terms of volume) and complex. It is also assumed that the transutural pore system functioned as the major respiratory system in the animal. The lack of external papillae or the absence of the water vascular system in the arms probably necessitated a large volume system which functioned by gaseous exchange *via* stromal tissues. In what seem to be more advanced genera (i.e., forms without transutural slits) respiration must have taken place across the entire plate and arm surfaces. As pointed out by Sprinkle (1973, p. 184), these forms usually have thinner plates. The nature of the internal water vascular system is unknown, but must have been extensive enough to handle the respiratory needs of the animal. The distinctness of each genus, and the lack of any transitional types between pored and nonpored genera, precludes discussion on how the evolutionary history of the loss of transutural slits was accomplished. *Amygdalocystites* has a transutural pore system that is reduced from that of *Sinclairocystis* or *Oklahomacystis*, but it is still a prominent, non-obsolete system.

In paracrinoid genera with epithelial arms, the underlying thecal plates are not altered in shape, and even when sutural pores are present these structures are not affected. This non-effect of arms

⁴ "Epistereom" is here used to denote the thin stereom covering over the transverse pore structures (especially adjacent to the suture) which is missing in many specimens that are slightly weathered. No distinct layer in terms of composition or density is implied. Indeed, examination of plates has shown them to be homogeneous in composition. Thus, "epistereom" and "mesostereom" are used as descriptive terms for the thickness of the plate. These terms are equivalent to "Epitheca" and "Stereotheca" respectively, as used by Kesling (1968, p. 274).





Text-fig. 1. Reconstruction and inferred living position of *Amygdalocystites florealis* E. Billings. Illustrates the well-developed pinnules and their covering plates, the covering plates on the recumbent arms and the stellate prosopon patterns on the thecal plates. The canted theca is probably an adaptation to living in currents (Plate 4, figs. 6, 7).

over plates indicates that the arms and thecal plates were not secreted in this juxtaposed position by the same layer of mesodermal tissue, *i.e.*, the arms were secreted by mesodermal tissue directly associated with the subventive appendages, and the thecal plates by thecal mesodermal tissue. The mode of preservation in some two-armed, recumbent-armed species appears to demonstrate that the connection between arm and theca was not particularly intimate or strongly adherent. This is especially true toward the distal ends of the arms where the arm lumens are reduced in size. Proximally the ossicles may be deeply impressed between the thecal plates. Where arm ossicles are missing, the smooth underlying callus is often undisturbed and shows no evidence of fracture. The possibility exists that (especially) the adthecal part of the lumen may have been lined with two distinct mesodermal tissues, their juncture occurring along the thecal plate-arm sutures. The epidermal tissue would probably have been resorbed. This resorption and the contact of mesodermal tissue against mesodermal tissue may, in part, have been the mechanism which stimulated the growth of the underlying thecal plate callus. The fact that the arms do not always rest on the same aboral thecal plates in any one species indicates that the callus is a growth response to the overlying arms or, in the case of *Malocystites*, the recumbent pinnules (which are without lumens).

This variation in the position of epithecal arms may, in part, be caused by the development of exothecal arms in early juveniles and may represent the primitive condition of the arms in this class. In the course of ontogeny the exothecal arms would begin to calcify and become recumbent on the theca with the pinnules directed upwards. The transversely oriented arms became fixed within a narrow arc extending from the peristome. The arc was wide enough so that the right arm, in post fixation growth along the theca, could extend either in front of or in back of the anal pyramid in some genera. In cases where the right arm is posterior to the periproct, the latter structure is to be found on the anterior face, *e.g.*, on some specimens of *Amygdalocystites* and *Sinclairocystis*. In the more specialized genera *Wellerocystis* and *Malocystites*, epithecal arms or pinnules are more strongly adherent to the theca; in the latter genus pinnule ossicle scars or imprints are common on the calluses. In these genera the arms branch close to the peristome and the periproct is

always on the same face. In *Platycystites* (herein considered a specialized genus) the calluses bear faint ossicle imprints, the periproct is always posterior, and the arms are generally fixed in position, on the upper part of the theca, relative to the ordered thecal plates.

In virtually all paracrinoid genera with epithecal arms, the inferred hydropore slit and the gonopore are consistent in location and morphology. It is the hydropore in "cystoids" which defines the anterior-posterior plane with the peristome (Bather's Madreporite plane or M plane) and not the periproct, according to Foerste (1916, p. 76). In paracrinoids, the gonopore is in the sagittal plane of symmetry. Hence, there is a gonopore plane, or G plane, which apparently is unique to the paracrinoids. The two openings are closely juxtaposed, however, and the difference is a minor one. The gonopore is situated on an elevated, conical pustule located on that portion of the central posterior peristomal plate that forms the peristomal lip. Normally the hydropore is located at the juncture of three plates, *i.e.*, the right lateral peristomal, posterior peristomal and a thecal plate. The slit is typically nearly parallel to the right (epithecal) food groove, but in some specimens it is at an angle to it. The slit is straight or slightly sinuate, and is slightly enlarged, in some specimens, where it crosses the plate suture. Rarely does the slit exceed three millimeters in length. Knowledge of these pores on paracrinoids with exothecal arms, *i.e.*, *Comarocystites* and *Achrado-cystites*, is limited.

The peristome, as far as can be determined, is formed by either four (most cases) or five plates. In the latter case, there are two plates on the anterior face and three on the posterior. In species with sutural pores, the normal pore structures are on the proximal (aboral) sutures of the peristomals. This suggests, along with their outlines, that the peristomal series is a slightly altered set of thecal plates.

Column. — Paracrinoids have a characteristic column which is distinct from that of other crinozoans. In genera where the column is known, *e.g.*, *Comarocystites*, *Amygdalocystites*, and *Platycystites*, each columnal is thin and entire, *i.e.*, not pentagonally subdivided as in crinoids. The articulatory surfaces of each columnal are finely crenulate and the overall appearance is similar to that of the blastoid

column. Thickness of the column is relatively constant throughout its entire length. A small lumen extends through the center of the column. The tightness of the suturing and the relatively broad articulatory surfaces, because of the small lumen, suggests a structure of limited flexibility.

Some genera with elongated, apparently straight columns, *viz.*, *Comarocystites*, and an attachment base must have had some flexibility to cope with bottom currents. Genera such as *Amygdalocystites* and *Platycystites* have a rigid bend, *i.e.*, ankylosed segments, in the proximal column which aided in orienting the peristome uppermost in the living animal.

In summary, the following morphological features are characteristic of the Paracrinoidea. With the exception of *Comarocystites* and *Achradocystites* (not studied) all paracrinoids have epithelial arms, and this is reflected in the outline below.

Outline of Characteristic Morphological Traits

- | | |
|--------------|---|
| I. Theca. | <ol style="list-style-type: none"> 1. Cystoid-like overall 2. Three basals 3. With or without internally opening, transutural slits or pores (ordinal taxobasis) 4. Typically more plates on right side 5. Peristome and column attachment offset to the left 6. Arm calluses 7. Gonopore and hydropore or posterior lip of peristome 8. Gonopore and peristome define "G" plane of symmetry 9. Plate growth by primary overlaying |
| II. Arms. | <ol style="list-style-type: none"> 1. Uniserial, with uniserial pinnules extending from each ossicle 2. Proximal or primary pinnule enlarged 3. Main food groove anterior on left arm(s), posterior on right arm(s) 4. Arm lumen expanded in (at least) proximal ossicles and floored by the channel in the arm callus |
| III. Column. | <ol style="list-style-type: none"> 1. Blastoid-like, ossicles short, holomorous, articulating surfaces crenulate 2. Proximal part bent, probably to orient peristome uppermost |

Morphological and habitus orientation. — Regnéll (1945) did not indicate what he considered to be the morphological orientation of this group. Billings (1854, 1858), Haeckel (1896), and Hudson (1905, 1911) oriented species of Paracrinoidea with the anal pyramid in a posterior position. Subsequently, the arms are referred to as anterior and posterior. In this orientation the hydropore slit and the gonopore are on the left side and not between the peristome and periproct. There are serious doubts that this orientation reflects the basic symmetry of this and other primitive echinoderm groups.

Foerste (1916, p. 76) proposed a more reliable system for the "cystoids" which in this case includes the paracrinoids:

"The orientation of the cystids is determined, not by location of the mouth and anus but by the vertical plane passing through the mouth and hydropore. The hydropore is regarded as occupying a position directly posterior to the mouth."

Foerste's system, used herein, is slightly modified in the paracrinoids; the gonopore is used instead of the hydropore. The two pores are closely juxtaposed, as mentioned above, and the difference is of minor importance in establishing orientation. Both hydropore and gonopore are rarely displaced from an adoral posterior position.

Foerste did not mention that in many "cystoids" the periproct is displaced toward the right. In paracrinoids the periproct is commonly shifted to the right and is located near the abcolumnal extremity of the theca. (Sprinkle, 1973, p. 184).⁵ In some cases the anal deflection goes so far that the anal pyramid is on the anterior face in some specimens of *Amygdalocystites* and *Sinclairocystis* and is generally the case in *Oklahomacystis*.

The longitudinal symmetry in paracrinoids with epithelial arms, as defined by the G plane, is distorted to asymmetry by the transverse offset of the peristome and the base of column attachment to the left. This results in an elongated right side and a compressed left side of the theca. The right arm(s) is typically longer and passes over the distal extremity of the theca in most specimens. The peristome is offset sub-laterally. Genera such as *Wellerocystis* and *Malocystites* have less peristomal offset, though some is indicated by the angle of insertion of the column. Little offset is visible in the exothecally brachiate *Comarocystites* in which the peristome is nearly centered over the medial column.

The life position of most, if not all, paracrinoids seems to have been with the peristome uppermost and the periproct at the same level or slightly lower. This is substantiated by genera such as *Amygdalocystites* and *Platycystites* in which specimens with the proximal column preserved generally have a markedly rigid adthecal

⁵ Anal migration from the posterior-crinoidal plane to the right, common in many primitive echinoderms with a dorso-ventrally elongated and inflated theca, may be caused by selective pressures to remove anal wastes from the hydropore-gonopore area. The deleterious effect of possible anal contamination to the subvective system may be of little importance.

flexure in the column. This flexure in an otherwise vertical column would cant the theca to the right, resulting in the uppermost, or near uppermost, position of the peristome.

J. W. Durham (oral communication) believes this flexure helped the column serve as a subsurface anchor (Text-fig. 6). He has observed that when a specimen is placed in the life position stated above, the epithecal arms (especially) in two-armed genera terminate in a horizontal plane, which is presumedly at the water-substrate interface. Durham feels that on some specimens of *Platycystites* there is a discernible difference in prosopon below this termination plane. He attributes this to the partial burial of the theca. Examination of other specimens of *Platycystites* by the authors, plus all of the other paracrinoid genera, has failed to reveal any such change in prosopon. The length of known columns, their lack of taper distal to the proximal flexure, and the presence of attachment discs (*Comarocystites*) also weigh against this interpretation. Also, it must be pointed out that arms sometimes do extend below the horizontal plane, e.g., in *Platycystites*, and onto the column.

We are reasonably sure that the theca was raised off the sea bottom by the column and was proximally bent (in recumbent armed forms) so that the peristome was uppermost in life. Beyond this our knowledge of their paleoecology is limited and must be inferred by their probable functional morphology. The offset of the theca, generally recumbent arms and compressed cross-section of many genera, suggests rheophilic organisms. These features would lend stability in a moderate unidirectional current.

Comarocystites with known exothecal arms probably formed a limited to full mucus net similar to that of contemporary crinoids (Lane and Breimer, 1974).

Genera with epithecal arms had only exothecal pinnules for subvection (*Malocystites*, which has both recumbent arms and recumbent pinnules, is discussed elsewhere in this paper). Normally the left side of the theca faced into the prevailing current. In two-armed species this would place the food grooves on the pinnules of the left arm on the lee side and they would be open to the back eddies caused by the pinnules. This coincides with similar observations by Meyer (1973) and Macurda (1973, 1974) who pointed out

that food grooves on rheophilic crinoids are maintained in a down-current position. The pinnule grooves on the right arm faced or opened up-current, but probably into considerably slowed water/back eddies caused by the proximal pinnules of the left arm. The large primary pinnules of both arms probably were effective in slowing the current. The more distal pinnules of the right arm would have been in the slow water/back eddies caused by the off-set theca. Thus the thecal off-set may have had more than a simple stability function.

Multi-armed genera may have fed in a way similar to two-armed genera, *i.e.*, *Oklahomacystis*, or as in the case of *Wellerocystis*, with numerous recumbent arms and exothecal pinnules, in a manner similar to blastoids or dactylocystid diploporids (Cystoidea). Our lack of knowledge of the pinnules and the columns in multi-armed genera limits our interpretation.

The probable lack of tube feet in the food grooves of the arms and pinnules suggests that paracrinoids were ciliary-mucoid feeders.

CLASSIFICATION

Kesling (1968, pp. 274-276), in his review of the classification of the paracrinoids, noted that "taxonomy of the Paracrinioidea is not yet satisfactory."

It is clear that Jaekel (1900, 1918) and Foerste (1916, 1920 a,b) recognized the distinctness of this "cystoid" group. Jaekel (1900, pp. 673-677) placed the known paracrinoids (*Malocystites*, *Canadocystis*, *Amygdalocystites*, *Comarocystites*, and *Achrado-cystites*) in his order Eustelea and informally placed them temporarily in a special order of the class Carpoidea. He later (Jaekel, 1918, p. 27) revised his stand and placed them in the order Deviata, subclass Eocrinioidea.

Foerste (1916, 1920,a,b) recognized the mutual affinities of *Malocystites*, *Canadocystis*, *Amygdalocystites*, *Comarocystites*, and *Wellerocystis* and placed them in the Cystoidea. Regnéll (1945) formalized the distinctness of this group of genera by erecting the class Paracrinioidea.

Attempts to create ordinal and familial taxa for paracrinoids have been unsatisfactory. Groupings by Bather, 1900, Jaekel, 1900, and Bassler, 1950, have resulted in inconsistent and incompatible relationships. Bather (1900, pp. 55-58) established the Malocystidae

[sic] (*Malocystites* and *Amygdalocystites*), and Comarocystidae [sic] (*Comarocystites* and *Achradocystites*). He placed them in the cystoid order Rhombifera. Jaekel (*op. cit.*) divided the Eustelea into two orders which were primarily based on the presence of free or recumbent arms. Members of his order Brachiata have exothecal arms and a central peristome; members of the Varicata have epithelial (recumbent) arms and an off-center peristome. This ordinal classification was used by Kesling (1968) in Part S of the *Treatise on Invertebrate Paleontology*.

Jaekel (*op. cit.*) also used the family Malocystidae but changed its definition to include the compressed, biconvex genus *Amygdalocystites*. He removed the family from the Rhombifera where it had been placed by Bather (*op. cit.*). Jaekel (1900, pp. 675, 676) erected the family Amygdalocystidae [sic] for *Amygdalocystites* and *Canadocystis*, both of which have two recumbent arms.

Bassler (1943, pp. 695-698) placed *Platycystites* in the Malocystitidae, a relationship which does not seem compatible for reasons given below. In 1950 he (Bassler, pp. 274-275) placed *Billingocystis* in the Malocystitidae and *Schuchertocystis* in the Comarocystitidae. Neither genus is herein considered a paracrinoid.

Kesling (1968) modified the familial taxa in accordance with Jaekel's (1900) definitions. In the order Varicata he included the families Malocystitidae (*Malocystites* and *Wellerocystis*) and Amygdalocystitidae (*Amygdalocystites*, *Canadocystis*, and *Sinclairiocystis*). In the order Brachiata he recognized the single family Comarocystitidae (*Comarocystites*, *Schuchertocystis* and *Billingocystis*). The genera *Achradocystites* and *Platycystites* were placed in "order and family uncertain."

In light of the present work covering most of the paracrinoid genera, modifications in the existing suprageneric taxa are necessary. The recumbence or freedom of the arms, as used by Jaekel, 1900, and Kesling, 1968, appears not to be a valid phylogenetic basis to ordinarily subdivide the class. Recumbence of the arms has independently occurred several times in the Paracrinioidea, as it has in the cystoids.

Of apparently basic importance in the paracrinoids is the plate structure, especially the presence or absence of sutural pores. Pore structures are not uniform in their structure, but they do indicate

that, in some genera, inferred parts of the hydrovascular system intruded between and altered the under and lateral (transutural) surfaces of the thecal plates. Grouping genera with modifications of a transutural water vascular system into a common higher taxon is apparently more natural than grouping genera without such structures with those that do have them. Usually other characteristics, in addition to plate types, are evident to aid in establishing orders.

The genera *Comarocystites*, *Sinclairocystis*, *Amygdalocystites*, *Oklahomacystis*, and *Achradocystites* have well-developed transverse lamellae and transutural pores on the inner and lateral surfaces of the thecal plates. *Comarocystites*, *Sinclairocystis* and, to a lesser degree, *Oklahomacystis*, new. (= *Amygdalocystites tribrachiatum*) also have externally concave plates and inflated thecae. These (five) genera are placed in the order *Comarocystitida*, new.

Genera without sutural pore structures typically have branched, recumbent arms or pinnules, small column attachments, and the thecal plates tend to be relatively smooth. These genera, *Malocystites*, *Wellerocystis*, *Canadocystis*, and *Platycystites*, are here placed in the order *Platycystitida*, new.

The polyplated *Comarocystitidae* probably is the more primitive order because several species have numerous transutural pores across each facet and exothecal arms. e.g., species of *Comarocystites*. The *Platycystitida* is probably derived from the *Comarocystitida* by the loss of pore structures and reduction in the number of thecal plates. Typically the arms in the platycystitids are far more solidly attached to the theca, and the more specialized forms, i.e., *Malocystites* and *Wellerocystis*, have, respectively, recumbent pinnules or distally branched arms.

SYSTEMATICS

Subphylum PARACRINOZOA, new

Diagnosis. — Characteristics are the same as the class *Paracrinoidea*.

Range. — Same as class *Paracrinoidea*, Middle Ordovician, North America, east of the 100th meridian, and Estonia; Upper Ordovician, Scotland.

This subphylum is established on the basis that its characteristics preclude its inclusion in either the *Crinozoa* Matsumoto, 1929,

or the Blastozoa Sprinkle, 1973. Paracrinozoans have characteristics that fit into both subphyla mentioned above and they also have traits which are peculiar to their own subphylum, *e.g.*, internally opening transutural slits, left lateral offset of peristome relative to the column, along with a pronounced plate increase on the right lateral margin and bilateral symmetry defined by the G plane.

The Paracrinozoa does not appear to be ancestral to, or share common ancestry with any other known echinoderm group.

Class PARACRINOIDEA Regnéll, 1945

[Order Eustelea Jaekel, 1900: Order Deviata Jaekel, 1918]

Diagnosis. — Essentially bilaterally symmetrical echinoderms with cystoid-like thecae, three basals, usually four peristomals; peristome and column offset toward the left side of the theca in the transverse plane; symmetry defined by the G plane (symmetry plane passing through the peristome and the gonopore), gonopore and hydropore posterior to peristome, hydropore slit at juncture of two peristomals and one thecal plate; with or without internally opening transverse sutural slits which variously extend through the thickness of the plates but do not open to the exterior or connect with neighboring slits; right lateral portion of the theca generally somewhat protuberant with increased intercalate plating; plates grow by overlayering in the crinozoan manner.

Arms uniserial with uniserial pinnules on each arm ossicle; arms exothecal or epithecal; in forms with epithecal arms the right arm(s) has a posteriorly facing food groove, on the left arm(s) the food groove is anterior; the proximal or primary arm ossicle is significantly larger than those adjacent, the primary pinnule is also larger; arm and pinnule food grooves covered by biserial covering plates; arms with lumens connecting to interior of theca, lumens sometimes distally reduced in size; in epithecal forms arms (and lumens) floored by raised callus of thecal origin, no internal lumen in pinnules.

Column blastoid-like, frequently rigidly curved close to proximal end of the theca.

Range. — Same as that given for subphylum Paracrinozoa above.

The ordinal classification of the Paracrinoidea is new and based

on the presence or absence of transutural slit structures. Seemingly close relationships between near homeomorphic genera, as the pored *Amygdalocystites* and the nonpored *Platycystites*, do not hold up when carefully analyzed. Jaekel's (1900) ordinal classification based on the presence of free or recumbent arms is not valid. Under such a scheme the closely related genera *Comarocystites* and *Sinclairocystis* would be placed in separate orders instead of in the same family, as recognized herein. Under the new ordinal scheme the included families are seemingly more closely interrelated.

Order COMAROCYSTITIDA new

[Palaeocystida Haeckel, 1896 (*pars*); Fungocystida Haeckel, 1896 (*pars*); Comarocystidae Bather, 1899, 1900 (*pars*); Malocystidae Bather, 1899, 1900 (*pars*); Amygdalocystidae Jaekel, 1900 (*pars*); suborder Brachiata Jaekel, 1900 (*pars*); Malocystidae Zittel, 1903 (*pro* Malocystitidae Bather) (*pars*); Malocystidae (Bather) Springer, 1913 (*pars*); order Deviata Jaekel, 1918 (*pars*); Malocystitidae Bassler, 1943 (*pars*); Comarocystitidae Bassler, 1950 (*pars*).]

This order can be diagnosed as follows. —

Paracrinoids with transversely elongated sutural pores; arms exothecal or epithecal (recumbent); thecal plates numerous.

The following families and genera are included in the order Comarocystitida:

Families	Genera
Comarocystitidae Bather, 1899	<i>Comarocystites</i> Billings, 1854 <i>Sinclairocystis</i> Bassler, 1950
Amygdalocystitidae Jaekel, 1900	<i>Amygdalocystites</i> Billings, 1854 = <i>Ottawacystites</i> Wilson, 1946 <i>Oklahomacystis</i> , new <i>Achradocystites</i> Volborth, 1870

Discussion. — The primordial paracrinoid was, in all probability, polyplated, with sutural pores along the margins of most of the thecal plates. The subvective system was transversely oriented, and the uniserial arms were exothecal without, or with only incipient, pinnulation. The primary transverse ambulacra suggest that the primitive number of arms is two, but their aboral branching probably

occurred at various times in the phylogeny of the class. Within the Comarocystitida, the general trend toward recumbency of the arms was established early, as was the torsional effect in the transverse plane. Also established in this group was the trend toward fewer and larger thecal plates. This is carried out to its greatest degree in the Platycystitida. The reduction of sutural pores is also found in this order in *Amygdalocystites*.

Family **COMAROCYSTITIDAE** Bather, 1899, emend.

[Nom. correct. Bassler, 1938, *pro.* Comarocystidae Bather, 1899]

Diagnosis.—Comarocystitida with concave thecal plates; sutural pores numerous; arms exothecal or epithecal.

Discussion.—Included in this family are the genera *Comarocystites* and *Sinclairocystis*.

This family, as emended, is now defined more on thecal characteristics than on whether the arms are free or recumbent. (Kesling, 1968, p. 282.)

As in virtually all paracrinoids, this family is essentially restricted to the Middle Ordovician of North America. *Comarocystites* is known from the Ottawa area in southern Canada; High Bridge, Kentucky; and Cape Girardeau, Missouri. *Sinclairocystis* is known only from Oklahoma. Paul (1967, pp. 474-477) described several internal molds of *Comarocystites*-like plates from the Starfish Bed, Upper Drummock Group of Girvan, Scotland, which is Upper Ordovician in age. This occurrence indicates that paracrinoids, which were not common in the Middle Ordovician, survived and extended their geographic range in the Upper Ordovician.

Genus **COMAROCYSTITES** E. Billings, 1854

Types-species: *Comarocystites punctatus* Billings, E., 1854.

- 1854. *Comarocystites* Billings, E. Canadian Jour., vol. 2, pp. 268-270, figs. 1-3.
- 1858. *Comarocystites* Billings, E. Billings, E., Canada Geol. Sur., Canadian Organic Remains, Dec. 3, p. 61, pl. 5, figs. 1-2.
- 1865. *Comarocystites* Billings, Meek, and Worthen, Acad. Nat. Sci., Philadelphia, Proc., vol. 17, pp. 143-145.
- 1868. *Comarocystites* Billings, Meek, and Worthen, Geology and Paleontology, vol. 3, Geol. Sur. Ohio, pp. 291-294, pl. 1, figs. 1a,b, 2a,b.
- 1880. *Comarocystites* Billings, Grant, Ottawa Field Nat., Trans., No. 1, pp. 29-30, pl. 1, figs. 1-5.

1891. *Comarocystis* Billings, Carpenter, Linn. Soc. London, Jour. Zool., vol. 24, p. 27.
1896(1895). *Comarocystis* Billings, Haeckel, Jena Zeit., Bd. 30, pp. 397-398.
1896. *Comarocystis* Billings, Haeckel, Die Amphorideen und Cystoideen, Fest. v. C. Gegenbaur, vol. 1, Leipzig, p. 70.
1900. *Comarocystis* Billings, Bather, Treatise on Zoology, vol. 3, p. 55. London.
1900. *Comarocystites* Billings, Jaekel, Deutsch Geol. Gesell., Zeit., Bd. 52, Hft. 4, p. 676.
1916. *Comarocystites* Billings, Foerste, Ottawa Nat., vol. 30, pp. 69-79, 85-93, 101-110, 112-113, figs. 1-6, pls. 2-5.
1918. *Comarocystites* Billings, Jaekel, Pal. Zeit., Bd. 3, p. 27.
1945. *Comarocystites* Billings, Regnéll, Lunds. Geol. Min. Inst., Medd., No. 108, pp. 37-40.
1946. *Comarocystites* Billings, Wilson, Canada Dept. Mines, Res., Canada Geol. Surv., No. 4, p. 11.
1965. [?] *Comarocystites* Billings, Paul, Geol. Mag., vol. 102, No. 6, pp. 474-477, pl. 20.
1968. *Comarocystites* Billings, Kesling, Treatise on Invertebrate Paleontology, Part S (1), pp. 282-287, figs. 166-168.

Diagnosis. — Theca fusiform to pyriform in profile, circular in cross section; most thecal plates hexagonal, typically exteriorly concave; sutures on the elevated peripheries, typically arranged in irregular vertical series; lateral and inner surfaces of thecal plates with well-developed subepistereomal sutural pores, manifest as lamellae and spaces of equal width; three small basals. Transverse food groove and mouth covered by biserially opposed covering plates. Three or four uniserial, exothecal arms branch from short, sessile food groove. Column of numerous depressed columnals with finely crenulate sutures, devoid of pentamerism.

Range. — *Comarocystites* is known from the Middle Ordovician of Missouri (Kimmswick Limestone); Ontario (Hull Limestone); and Kentucky (Curdsville Limestone). An occurrence of large *Comarocystites*-like plates is known from the Upper Ordovician (Ashgill), Upper Drummuck Group, of Girvan, Scotland.

Description. — The profile of the theca varies from pyriform-suboval to nearly fusiform; the cross section is nearly circular, becoming elliptical apically.

Foerste (1916, pp. 78-79, text-fig. 13) reported that there are between 11 to 15 basals in the specimens he examined and not three as reported by Billings (1854, p. 269). However, the basal area of most specimens is poorly preserved and the possible three basals may be radially fractured, giving a polybasal effect (Pl. 2, fig. 2). The basals, however, are short in this genus, and Foerste may have

been counting suprabasal intercalates. In all specimens of *Comarocystites* where the column attachment area is intact, Billings is seen to be correct. Indeed, three basals appears to be characteristic of the Paracrinoidea.

Considerable variation exists in the number of horizontal series of thecal plates, ranging, *vide* Meek and Worthen (1865, p. 143), from five to fifteen. Subsequent study verifies these figures, although nearly all have eight to fifteen rows. Virtually all specimens exhibit poorly developed vertical plate series, typically with apparent intercalated plates which affect both horizontal and vertical alignment. The only uniformity in plate arrangement, as noted by Foerste (*ibid.*, pp. 77-78), occurs around the peristome and periproct. The number of thecal plates varies with the species but ranges from *c.* 65 to over 225. Most thecal plates are hexagonal, but pentagonal and heptagonal plates, while not numerous, are not uncommon.

Each thecal plate is typically deeply concave on its external face, with the plate margins forming sharp crests (Pls. 1, 2). Internally each plate is correspondingly inwardly convex. Foerste (1916, p. 85) measured the thickness of the thecal plates in *C. punctatus* and stated their thickness as .5 - .6 mm at the center, while the mid-portion of each facet may be nearly 2 mm thick. This sharp difference is caused by peripheral growth coupled with the ontogenetic development of the transutural pore system.

The internal thecal plate structure was worked out in detail by Foerste (1916, pp. 85-87). In brief, the marginal and inner peripheral surfaces of each plate consist of a series of evenly spaced lamellae. They are confined to a triangular area extending from near the center of the plate to the corners or end of each facet. Each hexagonal plate has six such sets of lamellae. On larger specimens *c.* ten lamellae are present in each series. The central lamellae on each facet are longer than those lateral to them, hence, the convex inward shape of the plate margin. The plate corners are thin.

The lamellae from one plate extend across the suture and are in alignment with those on the adjacent plate. The inter-lamellar spaces are open to the interior of the theca but are covered by the outer portion of the "mesostereom" (footnote 4) and do not open to the exterior at the plate sutures in unweathered specimens. Penetrating this outer "mesostereom" area, according to Foerste (*op.*

cit.), are lunate pores which lead to depressions or planoconcave cavities just under the "epistereom." These pores connect the inter-lamellar spaces with the depressions. A pair of pores occupies each depression, but its included pores never open to the same inter-lamellar chamber, "being separated by one of the lamellae." Usually the pore depressions are arranged somewhat *en échelon* so that, for example, the right-hand pore of one pair and the left-hand pore of another will open into the same inter-lamellar space. Foerste (*ibid.*, p. 86) noted that "three of four pores belonging to different pairs may be connected to the same inter-lamellar space." Neither of the authors observed these lunate pores. There is some question of their existence.

The absence of lamellae and associated pores and depressions in the central portion of each plate indicates that these structures formed later than the early juvenile stages. A similar condition is also present in *Amygdalocystites* which is discussed below. Thecal plates in *Comarocystites* are similar to those of *Sinclairocystis*, except that the pores in the upper "mesostereom" and their sub-"epistereomal" depressions have not been observed in *Sinclairocystis*.

The four or five peristomal plates⁶ and the adjacent thecal plates are nearly of equal size. The peristome is located at the juncture of the four peristomal plates (Pl. 2, fig. 9). Typically, the peristomals and the large arm bases apparently formed a massive "plate" on which individual plate sutures are difficult to locate. The arm bases are typically callosities which cover the sutures of the thecal plates through which the lumens of the arms pass. (Foerste, *ibid.*, pp. 73-74.)

Each arm base resembles a truncated cone. Some specimens have an oval opening on their upper surfaces leading to the interior of the thecae (Pl. 1, fig. 4). These openings are the continuations of the arm lumens. Each foramen is slightly elevated and opens in a low, subconical boss. Between this boss and the marginal rim of the arm base is a shallow, rounded depression broken only where the sessile food groove crosses it. The shallow depressions are the arm sockets in which the exothecal arms articulate.

⁶ Kesling (1968, p. 282) noted that five peristomal plates are present. The authors have observed four and five, which may be due to poor preservation or generic (or species) variability.

Over the sessile transverse food groove is a biserially opposed series of covering plates which produce a sharply angled, serrated ridge or vault. Because they are so well preserved in several specimens, they were probably non-erectile. Observations by Foerste (*ibid.*, p. 77) and the authors indicate that the number of covering plate pairs over the unbranched portion of the transverse groove varies from eight or nine to fifteen or sixteen.

Foerste believed he had located the hydropore (*ibid.*, p. 74, text-fig. 2; p. 76) in some specimens, but it was not observed by the authors. He described it as a sinuous ridge between the right posterior peristomal plate and the adjacent lateral thecal plate. An opening which can tentatively be considered a gonopore is typically missing, but Foerste (*ibid.*, p. 76) believed there is evidence of a small gonopore pit just above the upper left-hand termination of this hydropore ridge. This would be in keeping with the location of the gonopore on all other paracrinoids.

The structure of the exothecal arms is known only in the type species *C. punctatus*, but is probably essentially the same in the two other herein recognized species. Each arm is composed of a single series of ossicles, each *c.* 60 percent longer than wide, and each supporting a single monoserial pinnule.⁷ The best preserved extant arm (*C. punctatus*, Pl. 1, fig. 2) has 11 articulated arm ossicles, and several more were undoubtedly present beyond the truncated tip. Total length of the arms was probably on the order of one and one-half times that of the theca. The pinnules are long and may extend up to half the length of the theca. The adthecal ones are composed of over 20 ossicles with nearly the same relative length-width ratio as the arm ossicles. The pinnules insert into the arms by shallow, rounded sockets with low, raised rims. Sockets closely situated to the theca have their axes tilted slightly upward, directing the pinnules away from the theca. But they, like the more distal pinnules which are normal to the arm axis, are directed inwards in an endotomous manner.

There is no evidence of food grooves on the arms, but there are covering plates on the pinnules. Several specimens (Pl. 2, fig. 8) show

⁷ It is interesting to note Haeckel's (1896, taf. 1, fig. 4) reconstruction of the type species *C. punctatus* with two opposed monoserial pinnules on each arm ossicle.

that for every two pinnule ossicles there are five pairs of covering plates.

The number of arms, contrary to previous authors, is variable, but with the limited number of available specimens it is undetermined whether this is a species characteristic. If, for example, *C. punctatus* can possess either one or two right arms, then *C. tribrachius*, n. sp., may well be a junior synonym. All of the available specimens of *C. shumardi* have four arm bases and the transverse food groove splits at both ends. Bifurcation in the transverse food groove on the right side cannot be demonstrated in *C. punctatus* even though the basal callus for arm support is large enough for the support of two arms. The single concave surface of this "basal socket," in addition to the unforked groove, strongly argues for a single azygous right arm. The single specimen of *C. tribrachius* has a definite, single right-hand "basal socket," a single lumen opening, an unforked food groove, and undoubtedly had only a single arm in this position.

The complete column is approximately twice as long as the theca. It was first described by Grant (1880, p. 29) in a specimen of *C. punctatus* (Pl. 1, fig. 3) which is the most complete specimen known. The column is composed of thin, circular, complete columnals which are radially furrowed on both upper and lower surfaces, giving a serrate intercolumnal suture. They are similar to those of blastoids. Its length is pierced by a narrow lumen. The column does not taper; at the distal end there is a slight flaring to form the attachment disk. No rhizoid-like extensions of the basal disk are known.

Comarocystites punctatus E. Billings Pl. 1, figs. 1-3; Pl. 2, fig. 8

- 1854. *Comarocystites punctatus* Billings, E., Canadian Jour., vol. 2, pp. 269-270, text-figs. 1-3.
- 1856. *Comarocystites punctatus* Billings, E., Billings, E., Geol. Sur. Canada, Rept. of Progress for the Years 1853-54-55-56, p. 288.
- 1858. *Comarocystites punctatus* Billings, E., Billings, E., Canadian Organic Remains, Dec. III, Canada Geol. Sur., pp. 61-63, pl. 5, figs. 1, 1a,b; 2, 2a,b.
- 1880. *Comarocystites punctatus* Billings, Grant, Ottawa Field Nat. Club, Trans., No. 1, p. 29, pl. 1, figs. 1-5.
- 1916. *Comarocystites punctatus* Billings, Foerste, Ottawa Nat., vol. 30, pp. 73-79, 85-93, pls. 2, 3, 5.
- 1946. *Comarocystites punctatus* Billings, Wilson, Canada Dept. Mines, Res., Geol. Sur., Bull. No. 4, p. 11.

Diagnosis. — Theca pyriform to fusiform in outline, transversely oval in cross section; typically more than eight vertical series be-

tween the basals and peristomals; total number of thecal plates *c.* 150; four (?three) pinnulated exothecal arms.

Range. — Middle Ordovician, Trentonian, Hull and Coburg beds of the Ottawa Limestone, Ottawa, Canada area.

Description. — A detailed description of *C. punctatus* would be largely repetitious of the generic description and of the work done by Foerste (1916, pp. 73-79, 85-93; pls. 2, 3 and 5).

Discussion. — Differentiation of species traits is difficult in this genus primarily because of 1) the lack of material, 2) the incompleteness of most specimens, and 3) the inability as yet to determine normal species variation. Of definite taxonomic value, and the most reliable species taxobasis (considering the usual state of the material), is the number of thecal plates in each vertical series. The number always exceeds eight plates; nine and ten plates are common in *C. punctatus*.

The indeterminate nature of the arm attachments makes this morphologic feature, at present, unreliable, *i.e.*, the right-hand attachment(s) suggests either a large, single arm or a tightly paired, double arm configuration. Because this is the only species of the genus with preserved arms and column, their characteristics are, at present, necessarily generic also.

***Comarocystites tribrachius*, n. sp.**

Pl. 1, figs. 4-6; Text-fig. 2

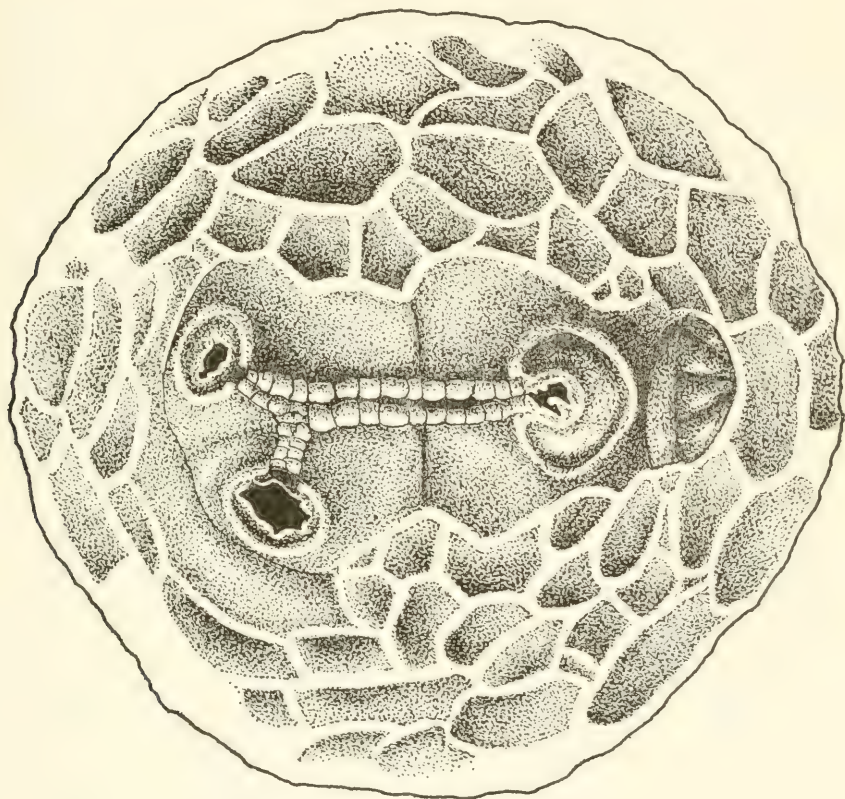
Diagnosis. — Theca composed of *c.* 220 plates arranged in *c.* 13 horizontal series of thecal plates; with three well-defined arm bases, the right arm base single, larger than either of the left-hand arm bases.

Range. — Middle Ordovician, Trentonian, in Curdsville Limestone, three and one-half miles south of High Bridge, Kentucky.

Description. — This species is based on a unique specimen which in general outline is fusiform and similar to some specimens of *C. punctatus* (*cf.* Foerste, 1916, pl. 2, fig. 2). In cross section it is transversely slightly compressed. The theca is composed of about 13 vertical series, with 15 to 17 plates in each series. The total number of thecal plates is about 220.

The vertical rows of thecal plates are obscured by the apparent intercalation of new plates at plate corners where three plates meet.

These intercalations are scattered over the thecal surface.⁸ The principal addition of thecal plates occurs, however, at the proximal end of the theca where the plates are smaller and have not developed the prominent, concave external surface.



Text-fig. 2. Dorsal view of *Comarocystites tribrachius*, n. sp., (Plate 1, fig. 4) showing the bifurcation of the left arm and the arm bases. Anal pyramid is adjacent and proximal to the right arm base. Openings in the arm bases are for the passage of the coelomic extensions from the theca into the arms.

⁸ These intercalations are not uncommon on the other species but seem to appear late in ontogeny, as evidenced by their absence in small specimens.

As in *C. punctatus*, the first thecal plate directly proximal to the periproctals is pentagonal.

Of apparently greatest taxonomic significance is the right-hand arm base which is definitely single and supported a larger arm than either of the paired left-hand bases. Also, the siliceous preservation clearly shows that the bases were perforate and that they allowed the passage of coelomic tissue extensions into the arms in somewhat the same manner as in crinoids.

In all other aspects this species seems to be much the same as the type species.

Discussion.— This species is similar to *C. punctatus*. Unless it is shown that *C. punctatus* does have three exothecal arms, not four, or that natural variation of that species includes three and four-armed types, the two species must be regarded as distinct. The number of plate series alone may be sufficient to differentiate *C. tribrachius*.

While the specimen of *C. tribrachius* is smaller than most examples of *C. punctatus*, its unusually high number of plate series and numerous plate intercalations suggests a late, mature (?gerontic) specimen.

Comarocystites shumardi Meek and Worthen, 1868 Pl. 2, figs. 1-7

- 1865. *Comarocystites shumardi* Meek and Worthen, Acad. Nat. Sci., Philadelphia, Proc., 1865, pp. 143-145.
- 1865. *Comarocystites shumardi* var. *obconicus* Meek and Worthen, *ibid.*, pp. 144-145.
- 1868. *Comarocystites shumardi* Meek and Worthen, Geol. Sur. Illinois, pp. 292-294, text-fig., pl. 1, fig. 1a, b.
- 1868. *Comarocystites shumardi* var. *obconicus* Meek and Worthen, *ibid.*, p. 294, pl. 1, fig. 2a, b.
- 1894. *Comarocystites shumardi* Meek and Worthen, Keyes, Paleontology of Missouri, pt. 1, Missouri Geol. Sur., vol. 4, p. 132, pl. 18, fig. 2.
- 1894. *Comarocystites obconicus* Meek and Worthen, Keyes, *ibid.*, p. 132, pl. 18, fig. 1.
- 1916. *Comarocystites shumardi* Meek and Worthen, Foerste, Ottawa Naturalist, vol. 30, No. 9, pp. 101-108, text-figs. 4, 5, 6, pl. 4, figs. 1a,b,c,d, 2, 3. [*C. shumardi* var. *obconicus* not recognized as distinct by Foerste, pp. 105-106.]
- 1920. *Comarocystites shumardi* Meek and Worthen, Foerste, Sci. Lab. Denison Univ., Jour., vol. 19, p. 195, pl. 22, figs. 24a,b.

Diagnosis.— Theca ovoid in profile and cross section; eight or less series of thecal plates; irregular intercalations of thecal plates in larger specimens; transverse food groove with paired arm bases at both ends.

Range.—Middle Ordovician, Trentonian, Kimmswick Limestone at Cape Girardeau, Missouri.

Description.—The distinctly oval outline does not occur in other species of *Comarocystites*, and most known specimens are small. Most do not exceed 25 to 30 mm in height.

The total number of thecal plates is 65 to 75. The number in larger specimens varies because of irregular intercalations of thecal plates. These intercalated plates disrupt the vertical alignment of plates found in juvenile specimens. Between the peristomals and the basals there are no more than eight series of thecal plates.

Foerste (1916, p. 101) correctly stated that the plates are "more deeply and more angularly concave" than those of *C. punctatus*. With more comparative material this trait may prove a valid and useful taxobasis. The general details of plate structure in *C. shumardi* are otherwise the same as in other species of *Comarocystites*.

There are two well-developed arm bases at each one of the bifurcated, sessile, transverse food groove. Details of the covering plates and exothecal arms are unknown.

There are five peristomals. The anterior lip is formed by two subequal, irregularly pentagonal plates; the posterior by a larger ?pentagonal plate. The lateral parts are the massive arm base plates which include the bifurcations of the main food groove.

Foerste (1916, p. 103, fig. 5; p. 104, fig. 6, pl. 4, fig. 1c) indicated the presence of a hydropore ridge on the posterior face, just to the right of the plane of symmetry and just under the right posterior arm base. This position is similar to that of other paracrinoids. Material available to the authors did not show this feature.

The periproctal area and column do not differ from those of the type species. It may be concluded that this species, while distinct, is close to *C. punctatus*.

Genus **SINCLAIROCYSTIS** Bassler, 1950

Type-species: *Sinclairocystis praedicta* Bassler, 1950.

Diagnosis.—Theca subspheroidal to nearly fusiform; nearly circular to broadly oval in cross section; composed of *c.* 37 generally hexagonal, externally concave plates; plates with slitlike subepistereomal sutural pores. Two recumbent, uniserial arms extend transversely from the peristome and both extend nearly to, or onto,

the basals. Peristome transversely oval, subapical; gonopore on its posterior lip; hydropore slitlike, juxtaposed to the right.

Range. — Middle Ordovician, Blackriverian, Bromide Formation, near top of the "green shale." All specimens are known from a single locality 1.8 miles south of Sulphur, Oklahoma.

Description. — The theca varies considerably in profile. It is typically subrounded to oval, though some specimens have a flat-tended upper surface. In cross section the theca is circular to transversely, broadly oval.

The theca plates, which number *c.* 37, are typically hexagonal, and are externally concave with elevated sutures. They closely resemble the thecal plates of *Comarocystites*.

Except for the basals and peristomals, the thecal plates are not arranged in any recognizable order. Plate number varies from 27 to 52 in observed specimens, with an average of 37. Thecal size (observed range from 8.2 to 20 mm high) is only slightly related to the number of thecal plates. Small specimens (*e.g.*, *c.* 10 mm high, 29 to 42 thecal plates) may have as many or more plates than larger specimens (*e.g.*, 13+ mm high : 28 to 36 plates). The largest observed specimen, approximately 20 mm high, has 52 plates. There is no observable basic juvenile plate pattern, as in *Canadocystis*, for example, and numerous intercalates can occur early in ontogeny. Sometimes large specimens have relatively few plates (*e.g.*, 13.5 mm high: 29 plates; 17.0 mm high : 31 plates), indicating high intra-species variation with regard to plate addition.

There is a definite preference for intercalates to form above the basals, especially in the lower, right-lateral part of the theca, and they are manifest as smaller, more numerous plates. (See discussion below concerning other paracrinoids with two epithecal arms, under *Platycystites* and *Canadocystis*.) The left-lateral, left, and central parts of the anterior and posterior faces have larger plates with little evidence of intercalation.

Slitlike sutural pores, completely roofed over by epistereom, are present on all thecal plates (Pl. 3, figs. 4-6). The number of pores on each side of a plate varies with the size of the plate and ranges from three to nine, with six and seven being the most common number (Pl. 3, figs. 1, 3, 7, 12). The average is slightly less than one pore

for every 0.4 mm of suture length, with the actual width of the pore averaging 0.16 mm. The length of each pore on the internal surface of the thecal plates varies because of the triangular arrangement of the pore field. The slitlike pores in the center of the field (essentially bisecting the adjacent plate suture) are the longest and oldest; those at the edges of the triangular field (near the plate corners) are the shortest and youngest. Like the pore structures in *Comarocystites*, they are completely open to the interior of the theca. Unweathered plates are externally covered with low, rounded tubercles which have an approximate radial alignment (Pl. 3, figs. 4-6).

The small, oval peristome is formed by three, and sometimes four, peristomals. In cases where there are three, there is a single pentagonal peristomal on the posterior and two irregularly shaped peristomals on the anterior face. The anterior peristomals extend under the recumbent arms, forming the lateral sides of the peristome. In cases where there are four peristomals, the pentagonal plate adjacent to the other posterior peristomal inserts into the peristome, forming the posterior right quadrant of the opening. In this case the anterior and posterior peristomals suture under the recumbent arms. The inter-peristomal sutures show no evidence of sutural pores, but where the peristomals are in contact with other thecal plates there are typical pores. The peripheral outline of the three peristomal condition is evenly hexagonal and covers nearly the same area as an adjacent thecal plate. While it is possible that the peristomal series represents a fractionated thecal plate, which would explain the lack of inter-peristomal pores, it would also mean the peristome fundamentally opens within or through a plate. It seems more likely that the oral series is reduced and shaped by the growth pattern of the adjacent thecal plates.

On the posterior lip of the peristome (posterior or left posterior peristomal) is the round, slightly elevated gonopore. In several specimens the gonopore is repeated; the second opening is slightly smaller and less elevated, and located just ventral to, or slightly offset to, the right (Pl. 3, fig. 9). Between the left posterior peristomal, the right posterior peristomal and the thecal plate that partly inserts between the two previous plates is the elevated, slitlike hydropore. It may lie either essentially parallel to the peristomal suture or

transversely across it. In some specimens the hydropore appears to be an incursion, albeit with some modification, of a sutural pore between three plates, while in others there is no obvious connection between the hydropore and the sutural pores.

In some specimens there is an anomalous gonopore-like opening which occurs near, or in the center of, a thecal plate (Pl. 3, figs. 1, 2, 6). Usually this opening, when present, is located ventral to the periproct and may be above or below the ambitus. Some specimens have an opening on the anterior face. This has been observed on thecal plates near the recumbent arm. Both the anterior and posterior pore can be present on the same specimen. The number of available specimens is limited, but it appears that this anomalous pore(s) occurs on approximately fifty percent of the specimens. Perhaps the presence or absence of these pores is due to sexual dimorphism.

The periproct is slightly subapical. It is usually found on the posterior face, but in some specimens it is on the anterior. It is bounded by a "periproctal" series of four thecal plates. A specimen figured by Strimple (1952, p. 159, fig. 7) shows six wedge-shaped periproct covering plates, forming a low, rounded, anal pyramid.

The positions of the uniserial, recumbent arms on the theca are variable; that of the right arm determines whether the periproct is on the anterior or posterior face.

The arms are uniform in height and width except near the tips, where they taper. Each arm consists of 15 to 22 ossicles. On top of each ossicle there is a concave, rounded pinnule seat from which extends a short food groove that terminates at the upper margin of the main food groove. All of these short (side) food grooves are parallel on the same arm and enter the main food groove on the same side of the arm. The short food grooves of the opposite arm always enter the main groove on the opposite side. In normal paracrinoid fashion, the side grooves of the left arm and the main food groove are on the anterior side of the arm; on the right arm they are on the posterior side. The main food groove is impressed into the side of the arm approximately one-third of the height of the arm above the adthecal base (Pl. 3, figs. 3, 6). No pinnules or covering plates over the food grooves are known.

The lumen is unusually large in the proximal arm segments. In

cross section, the lumen is ovoid to subclavate, with a small protuberance extending under the main food groove. The floor of the lumen is thecal callus material. The extent of the enlarged part of the lumen appears to be limited to the proximal four or five ossicles; distally the lumen is sharply reduced in size. In the distal part, the lumen appears to be a flattened, elliptical opening between the callus and basal part of the arm ossicle. Distally the arms are less likely to be preserved than proximally, perhaps indicating more or tighter contact proximally.

In fresh material, or on specimens where the arm ossicles are freshly broken off, there are no observed openings between the lumens and the interior of the theca. However, in specimens that are only slightly weathered, openings are visible, predictably occurring at the juncture of the anterior peristomals (which extend under the arms) and the adjacent thecal plates, and in the case of the right arm, in the suture above the periproct. In this case it appears to be a weathering feature and not the uncovering of a normal morphological feature. Distal to the enlarged lumen such openings do not occur, except for weathered sutural pores.

Underlying the arms are thecal calluses. They are apparently stimulated by the overlying arm(s) but are secreted by thecal tissues. The upper surface of each callus is slightly elevated above the thecal surface and provides an even platform for the arm. Thecal callus deposits are thickest in the middle of the concave thecal plates, and thinnest across the plate sutures. The calluses do not cover the sutures. This indicates their thecal origin. The upper surface of a callus is concave but is bounded by a pair of low, rounded ridges on the margins of this surface. Contact between the arm and the theca is on the tops and outside margins of these ridges. The mutually independent growth of the arms and the underlying thecal plates suggests that the arms were not "cemented" to the calluses but were tightly held in place by tissues.

The position of the off-center column attachment and basals, relative to the peristome, clearly indicates that torsion in the transverse plane has taken place, as in other paracrinoid genera. The column is unknown.

Discussion. — There is a striking similarity in the thecal plates of this genus and those of *Comarocystites*. In both cases the plates

are externally concave, hexagonal, and possess similar slitlike modifications of sutural pores along their periphery. *Sinclairocystis* does not seem to have the system of lunate depressions in the outer "mesostereom" with canals leading from pores in the depressions to the interlamellar space (sutural pores), as described in *Comarocystites* by Foerste (1916, pp. 85-87, 106). In both genera the stellate pattern on the interior surface of the thecal plates, caused by the development of the sutural pore system, is essentially the same. There is a tendency in *Sinclairocystis* for the adcentral portions of the older pores, i.e., those in the center of the pore fields, to become secondarily filled with stereom. This secondary filling apparently does not take place in *Comarocystites*. The rims of the thecal plates in *Sinclairocystis* are flattened and form broader sutural pore rows than those in *Comarocystites*. The epistereomal covering over the sutural pores is eroded away in most specimens and probably was thinner than in *Comarocystites*.

Growth of the arms over the theca varies considerably among specimens. The right arm is variable in position and may lie on either the anterior or posterior side of the periproct. Where the periproct is posterior to the right arm, the arm sometimes broadly curves onto the posterior face. In most cases, however, the arms are lateral and extend in a straight line toward the aboral end of the theca, except that some curvature is frequently seen on the distal ends.

Whether the periproct is anterior or posterior may depend upon the possible exothecal state of the arms in the juvenile. This would allow for variation caused by recumbency on different adoral thecal plates. Subsequent thecal growth would tend to place the arms at the transverse-lateral limits of the theca where the pinnules on the recumbent arms would have the greatest unobstructed field of sweep.

Strimple (1952, p. 160) used the position of the right arm as a species taxobasis. The current study indicates that the variable position of this arm is an intraspecific trait. He (*ibid.*) also used such traits as the number of thecal plates and thecal shape for species differentiation. The first of these must be used with care because of the inconsistency between thecal size and plate number. The second trait is largely dependent on the course of the recumbent arms across the theca. The species *S. angulatus* and *S. sulphurensis* were established by Strimple (1952, pp. 158-160) on these

taxobases and herein are considered synonymous with the type species *S. praedicta*. *Sinclairiocyctis angulatus* has a broadly curving right arm and the theca is expanded and flattened distally. *S. sulphurensis* is a small specimen with some juvenile characteristics, among them a smaller number of plates.

The variable course of either arm has an effect on the overall shape of the theca, *i.e.*, effecting a protuberant expansion under the arm. The mechanism for such "abnormal" thecal growth is unknown, except that it is a direct response to arm growth. Errant growth of arms in non-pored *Platycystites* has no effect on thecal shape.

In one specimen (Pl. 3, figs. 9, 10) the left arm bifurcates and the anterior branch of that arm is also distally bifurcated. The bifurcated arms share the same primary pinnule. The main food groove past the primary pinnule is anomalous in that the posterior branch has its groove on the (normal) anterior side, but the anterior branch has its main groove, along with its distal branch, on the anterior side. On the anterior face this anomalous specimen has a pair of gonopore-like openings on the left anterior peristomal plate.

This monospecific genus has considerable intraspecies variation. An early exothecal arm stage in young juveniles could explain variation in the recumbency of the arms and, as shown above, the position of the arms effects, to some degree, the variable thecal shape.

All of the known specimens of *Sinclairiocyctis* are topotypes. The specific splitting of the few specimens available, from what may have been a biocoenosis, seems ill-advised.

***Sinclairiocyctis praedicta* Bassler, 1950**

Pl. 3, figs. 1-12

1950. *Sinclairiocyctis praedicta* Bassler, Washington Acad. Sci., Jour., vol. 40, No. 9, p. 275, figs. 9, 10; p. 276.
 1952. *Sinclairiocyctis angulatus* Strimple, Washington Acad. Sci. Jour., vol. 42, No. 5, pp. 158, 160; p. 159, figs. 5-9.
 1952. *Sinclairiocyctis sulphurensis* Strimple, Washington Acad. Sci., Jour., vol. 42, No. 5, pp. 160, 159, figs. 1-4.

Diagnosis, range and description are the same as for the genus.

Family **AMYGDALOCYSTITIDAE** Jaekel, 1900 emend.

[Nom. correct. Kesling, 1968, *pro* Amygdalocystidae, Jaekel, 1900]

Diagnosis. — Comarocystitida with convex thecal plates; sutural

pores numerically reduced to *c.* two on each plate facet; two or three epithecal or exothecal arms.

Discussion.—This family includes the following genera: *Amygdalocystites*, *Oklahomacystis*, new, and *Achradocystites*.

The assignment of *Achradocystites* to this family is provisional, on the assumption that the three exothecal arms on *Achradocystites schmidtii* Hecker, 1958, were uniserial. However, there is some evidence which suggests that the arms may be biserial. In most known aspects this genus seems to be a paracrinoid. New material with the arms preserved might necessitate the establishment of a new family. In this case the emended definition of the Amygdalocystitidae would hold, except that all of the genera would have epithecal arms. This would move the emended definition of the family closer to the original concept of Jaekel.

Jaekel's definition of the Amygdalocystitida is here emended to include only those forms with sutural pores; hence, the non-porous *Canadocystis* is herein excluded.

All genera in this family are Middle Ordovician in age: *Amygdalocystites* is found in the Ottawa region of southern Canada, and High Bridge, Kentucky; *Oklahomacystis* is found in the Arbuckle Mountains of Oklahoma; and *Achradocystites* is found in horizons D_{II} and D_{III} (uppermost Middle Ordovician) in Estonia. The last genus is one of the few occurrences of a paracrinoid outside of North America.

Genus **AMYGDALOCYSTITES** E. Billings, 1854

Type-species: *Amygdalocystites florealis* Billings, 1854.

- 1854. *Amygdalocystites* Billings, E. Canadian Jour., vol. 2, pp. 270-271, figs. 4-9.
- 1856. *Amygdalocystites* Billings, E., Billings, E. Geol. Sur. Canada, Report for the years 1853-54-55-56, pp. 288-290.
- 1858. *Amygdalocystites* Billings, E., Billings, E., Geol. Sur. Canada, Canadian Organic Remains, Dec. III, pp. 63-65, pl. 6, figs. 1a-e, 2a-f, 3a, 6.
- 1879. *Amygdalocystites* Billings, Zittel, Handbuch der Paleontologie, Bd. 1, p. 413.
- 1891. *Amygdalocystis* Billings, Carpenter, Linn. Soc. London, Jour. Zool., vol. 24, p. 27.
- 1896. *Amygdalocystis* Billings, Haeckel, Die Amphorideen und Cystoideen, Fest. v. C. Gegenbaur, Bd. 1, p. 106, Leipzig.
- 1900. *Amygdalocystites* Billings, Jaekel, Deutsch Geol. Gesell., Zeit., Bd. 52, pp. 675, 676.
- 1900. *Amygdalocystis* Billings, Bather, Treatise on Zoology, vol. 3, p. 57, figs. 19, p. 58.
- 1913. *Amygdalocystites* Billings, Springer, in Zittel (Eastman, ed.) vol. 1, p. 151.

1918. *Amygdalocystis* Billings, Jaekel, Pal. Zeit., Bd. 3, p. 27.
1945. *Amygdalocystites* Billings, Regnéll, Lunds Geol.-Min. Inst., Medd., No. 108, pp. 38, 39.
1946. *Amygdalocystites* Billings, Wilson, Canada Dept. Mines Res., Bull. No. 4, pp. 9-11, pl. 1, figs. 1-4.
1946. *Ottawacystites* Wilson, *ibid.*, p. 14, pl. 3, fig. 1.
1968. *Amygdalocystites* Billings, Kesling, Treatise on Invertebrate Paleontology, Part S, pp. 278-279, p. 269, figs. 1-4.

Diagnosis. — Theca transversely elliptical in cross section, ovoid to almond-shaped in outline. Thecal plates numerous, hexagonal to octagonal, each plate with prominent prosopon rays radiating from an elevated central boss to the plate corners. Subepistereomal sutural pores well developed, usually adjacent to, or under, prosopon rays. Two uniserial arms recumbent, transverse. Each arm ossicle with free-standing pinnule; biserial covering plates on pinnules and over main food grooves. Periproct on anterior or posterior face. Column slightly tapering, composed of thin ossicles with crenulate sutures; proximal column sharply curved.

Range. — Middle Ordovician, Trentonian; Hull Formation, Ottawa, Ontario and Hull, Quebec area; Kirkfield Formation, Kirkfield, Ontario; Curdsville Limestone, Mercer County, Kentucky; and Blackriverian, Bromide Formation, Arbuckle Mountains, Oklahoma.

Description. — In antero-posterior outline the theca is typically somewhat almond-shaped. Cross-sectional outlines are biconvex.

The total number of thecal plates varies according to the size of the theca. Large specimens, which may exceed 25 mm in height, typically have over 100 thecal plates, Kesling (1968, p. 276) stated that 90 plates is an average number for this genus, but elsewhere (*op. cit.*, p. 278) gave a range of 90 to 180 thecal plates. Smaller specimens with 50 to 75 plates are not uncommon. There is no apparent order in the plate arrangement.

The theca contains three subequal basals; five peristomals, of which three are essentially posterior and two are anterior; and a varying number of periproctals, typically four to six.

Unweathered plates are typically hexagonal, with a circular, solid central area which is typically elevated into a low, rounded boss. Extending from this boss, under the epistereom covering, is a pair of elongated pore structures that extend to each plate facet. There are 12 such structures on each plate and each is continuous with like pores on adjacent plates. Each pair underlies, or lies on

either side of, a prosopon ray extending from the central boss to the mid-point of each facet. No external manifestations of pore structures are visible in unweathered plates (Pl. 4, fig. 3; Pl. 5, figs. 4, 5, 7).

The solid central area of a thecal plate is devoid of pore apparatus, suggesting that the development of the inferred internal hydrovascular tissues, or other respiratory tissues associated with the pores, occurred at a stage of ontogeny later than the juvenile, solid plate stage. Intercalated plates exhibit the same character. Other primitive echinoderms also exhibit a similar mode of development, *e.g.*, the eocrinoid *Gogia*.

Weathered *Amygdalocystites* plates are typically without the epistereom and display a stellate outline similar to sutural pore- (epispire-) bearing plates of some cystoids, eocrinoids and cornutans (Pl. 4, fig. 6). In this weathered state, the plates are of moderate thickness and the sutural pores, although reduced in number, are typically paracrinoid in their form. Inasmuch as most plates are hexagonal, each plate corner generally marks the confluence of three plates and the confluence of three radiating ridges. This commonly results in optical confusion (especially if the ridges are prominent) for this confluence resembles a bossed plate center. Close examination of the sutures obviates this error. Between the major ridges, in the type species, radiating accessory ridges may extend from the boss to the plate edge and align with those on opposing plates.

The gonopore is uniformly located on the posterior rim of the peristome (on the mid-posterior peristomal) and is manifest either as a simple pore or, more commonly, as an apically punctured frustum (Pl. 5, fig. 5). To the left of the gonopore, across the suture between the central and right posterior peristomals, is the raised hydropore slit which is parallel or subparallel to the closely situated, recumbent right arm. Both the hydropore and gonopore are similar in form and position to those of *Sinclairocystis* and *Platycystites*.

The periproct, as in other two-armed paracrinoids, is always near the right arm and may be on either the anterior or posterior face. The number of thecal plates incorporated into the periproctal series varies from four to six. The gently arched anal pyramid is typical of paracrinoids and is composed of *c.* eight triangular or wedge-shaped covering plates.

The transverse, uniserial, recumbent arms are structurally nearly the same as those of *Sinclairocystis* and *Platycystites*. Several specimens (Pl. 4, figs. 6, 7; and Pl. 4, fig. 5, the last being one described by Wilson, 1946, pl. 3, figs. 1a,b, as *Ottawacystites*) clearly show the free-standing pinnules and the covering plates on both the pinnules and the main food groove(s). The inter-relationship between these two series is unique to the paracrinoids. All of the platelets over the main grooves are essentially quadrangular and opposed. There is no evidence to support erectility, and the covering plates seem to have formed a fused roof over the main conduit. Platelets on the uniserial pinnules, on the other hand, are typically somewhat disarrayed in preservation. They were probably more loosely anchored and erectile. At the base of each pinnule, the distal covering plates over the main food groove seem to split and then extend up the pinnule as an alternating to subalternating series.⁹ These platelets are subtriangular at the base of the pinnular series but have a rectangular outline throughout most of the length of the pinnule. The platelets are subequal, typically with a smaller plate alternating with, or intercalating between, every second larger platelet. Pinnules are rarely preserved and a great deal of reliance must be placed on few specimens in describing them.

The longer of the arms, typically the left, extends nearly to the column. The right arm extends from the offset peristome, over the distal extremity of the theca, to approximately half-way down the length of the right side of the theca (Pl. 4, fig. 6). The arms taper slightly and are pointed or narrowly rounded at their ends. As in other two-armed epithecal paracrinoids, e.g., *Sinclairocystis* and *Platycystites*, the right arm has a posterior-facing main food groove, and an anterior-facing main groove is on the left arm. The lumen in the recumbent arms of paracrinoids has not been observed in *Amygdalocystites*. In virtually all specimens, the two adperistomal arm ossicles or primaries are larger and are higher than the others. Likewise, the adperistomal pinnules are thicker and longer than the other pinnules which aborally gradually diminish in size (Text-fig. 1; Pl. 4, fig. 6).

The column attachment seat, i.e., thecal basals, is typically off-

⁹ If this apparent relationship is true, it may indicate that pinnules are phylogenetically younger than the arms and developed as outgrowths from them.

set to the left, as is the peristome. The attachment is lateral and slightly distal to the proximal thecal extremity. The column is similar in composition and form to that of other paracrinoids. It is composed of short, whole columnals which are crenulate on their articulatory surfaces. The close fitting of the sutures resembles syzygy. This inferred rigidity derives from the consistent, pronounced curve to the right in the proximal portion of the column. This is effected by differential growth of the columnals. The curvature from the (apparently) straight column cants the theca so that the peristome and the adperistomal pinnules are uppermost. The ends of the recumbent arms, when the theca is in this position, terminate at a horizontal plane.

Discussion.—Although there are relatively few species known of *Amygdalocystites*, the genus may have been unduly subdivided on trivial or imaginary differences. *A. tenuistriatus* E. Billings, 1854, and *A. huntingtoni* Wetherby, 1881, are herein considered conspecific with *A. florealis*. *A. tenuistriatus* is known from only a few weathered scraps. One of these scraps bears plate prosopon similar to that of *A. florealis*. *Amygdalocystites huntingtoni*, contrary to Wetherby's (1881, p. 177) analysis, has arms and prosopon essentially identical to that of *A. florealis*. Specimens of this species vary in their modes of preservation. The unique, silicified specimen was found in the Curdsville Limestone at High Bridge, Kentucky (Pl. 5, figs. 1-3).

Amygdalocystites radiatus E. Billings (1854, p. 271) is a difficult species to resolve. Unweathered thecal plates of this poorly represented form have distinct, non-expanding prosopon rays, with pustules between them (Pl. 5, fig. 7). Specimens illustrated by Raymond (1921, pl. 2, figs. 5-7) and Wilson (1946, pl. 1, figs. 3, 4) show a slightly different kind of plate weathering than is usually seen in *A. florealis*. Establishing or identifying species on the basis of weathering seems ill-advised. For the present, the authors are willing to accept the individuality of *A. radiatus* on the basis of its prosopon, while recognizing that this is not always a valid taxobasis.

Amygdalocystites laevis W. R. Billings (1883, p. 52) is also an *Amygdalocystites* and was erroneously made the basis of a separate genus, *Ottawacystites*, by Wilson (1946, p. 14) on the basis of its "free (exothecal) arms," which actually are pinnules (Pl. 4, fig. 5).

Incipient sutural pores are present on the monotypic species, but apparently only one per facet is present. The small theca is apparently a juvenile; only the central boss of the thecal plates, with rudimentary pores, is present. If, in the course of ontogeny, this single pore bifurcates to form two on each facet, as typical in this genus, the specimen probably is assignable to *A. florealis*. In all other respects (arms, pinnules, column, thecal outline) it is indistinguishable from *A. florealis*.

Amygdalocystites ?gorgo Sinclair (1948, p. 313, pl. 42, fig. 8) is an exceedingly poorly preserved specimen from the Upper Trenton of Quebec. No other known specimens can be assigned to this species.

Amygdalocystites tribranchiatus Bassler (1943, pp. 695, 696) is most distinct. It bears three slightly impressed ambulacra; the left arm is branched near the peristome. While this species is related to *Amygdalocystites*, it is herein assigned to the genus *Oklahomacystis*, new.

Wilson (1946, pp. 9, 10) stated that *Amygdalocystites* bears "two large recumbent arms of different lengths; composed of a double series of plates, one beneath the other;" the bottom plate is supposedly "a rectangular prism" on which lies the second plate which is a "narrow recumbent cylinder, one side flush with the basal plate, the other having an [ambulacral] groove at the line of juncture of the two sections." Broken paracrinoid ambulacral arms under magnification show that the arm is uniserial, and examination of a number of specimens indicates *Amygdalocystites* is typical in its uniserial arm composition.

The pinnules (or brachioles, as Raymond, 1921, p. 3, called them) were reported by that author to be evenly biserial, having a structure similar to the arms of *Pleurocystites*. It is doubtful if this is indeed the case. A number of observations indicate that the pinnules, like the arms, are uniserial and have small covering plates over the subvective grooves.

***Amygdalocystites florealis* Billings, E., 1854**

Pl. 4, figs. 1-7; Pl. 5, figs. 1-7; Text-fig. 1

- 1854. *Amygdalocystites florealis* Billings, E., Canadian Jour., vol. 2, pp. 270-271, figs. 4-6.
- 1854. *Amygdalocystites tenuistriatus* Billings, E., Billings, E., *ibid.*, p. 271, fig. 9.
- 1856. *Amygdalocystites florealis* Billings, E., Billings, E., Geol. Sur. Canada, Rep. of Prog. for the Years 1853, 54, 55, 56, p. 289.

1856. *Amygdalocystites tenuistriatus* Billings, E., Billings, E., *ibid.*, pp. 289-290.
 1858. *Amygdalocystites florealis* Billings, E., Billings, E., Geol. Sur. Canada, Canadian Organic Remains, Dec. III, pp. 63-64, pl. 6, figs. 1a-e.
 1858. *Amygdalocystites tenuistriatus* Billings, E., Billings, E., *ibid.*, pp. 64-65, pl. 6, figs. 2a-f.
 1881. *Amygdalocystites huntingtoni* Wetherby, Cincinnati Soc. Nat. Hist., Jour., vol. 4, No. 2, p. 177, pl. 5, fig. 3.
 1883. *Amygdalocystites florealis* var. *laevis* Billings, E., Billings, W. R., Ottawa Field Nat. Club, Trans., No. 4, pp. 51-52.
 1896. *Amygdalocystis florealis* Billings, Haeckel, Die Amphorideen und Cystoideen, Fest. v. C. Gegenbaur, Leipzig, pp. 106-107, fig. 15.
 1900. *Amygdalocystis florealis* Billings, Bather, Treatise on Zoology, pt. 3, p. 57, fig. 19, London.
 1946. *Amygdalocystites florealis* Billings, Wilson, Canada Dept. Mines Rec., Geol. Sur. Bull. No. 4, pp. 9-10, pl. 1, figs. 1-2.
 1946. *Ottawacystites laevis* (Billings, W. R.), Wilson, *ibid.*, p. 14, pl. 3, figs. 1a-b.

Diagnosis.—Amygdaloid theca with two recumbent arms; thecal plates with expanding rays extending from rounded central boss to plate corners; smaller rays extending from boss to bisect plate facets.

Range.—Middle Ordovician, Trentonian; ?Hull Formation, Kirkfield, Cobourg Formation, Ottawa, Ontario; Curdsville Limestone, High Bridge area, Kentucky.

Description.—The detailed description of this type species of *Amygdalocystites* does not differ from the generic analysis given above, except for a few diagnostic traits. As indicated in the specific diagnosis, the plate prosopon is the principal taxobasis.

The prosopon rays expand in width and height toward each plate corner. Each ray is similar in plan to a limb of a Maltese Cross. At the juncture of almost any three plates, where the expanded ends of three rays meet, is the center of a raised triact which is sometimes the main prosopon expression on slightly weathered plates. Lesser, non-expanding prosopon rays extend from the central boss to bisect the plate facets and align themselves with like ridges on adjacent plates in "pectinirhomb" fashion.

The sutural pores, as seen in slightly weathered plates, typically directly underlie the radiating ridges, while in *A. radiatus* they underlie the inter-radial pustulose areas. Their structure has been discussed above.

Wilson (1946, p. 9) noted the variation in size of specimens from Canada, viz., height 30 to 45 mm, width 18 to 25 mm and thickness

12 to 15 mm. They are, on the average, slightly larger than the specimens found in the Curdsville Limestone of Kentucky.

***Amygdalocystites radiatus* E. Billings, 1854**

Pl. 5, fig. 7

- 1854. *Amygdalocystites radiatus* Billings, E., Canadian Jour. vol. 2, p. 271, figs. 7, 8.
- 1856. *Amygdalocystites radiatus* Billings, E., Geol. Sur. Canada, Rep. of Prog. for the Years 1853-54-55-56, p. 289.
- 1858. *Amygdalocystites radiatus* Billings, E., Geol. Sur. Canada, Canadian Organic Remains, Dec. III, p. 65, pl. 6, figs. 3a-b.
- 1883. *Amygdalocystites radiatus* Billings, E., Billings, W. R., Ottawa Field Nat. Club, Trans., No. 4, p. 51.
- 1921. *Amygdalocystites ?radiatus* Billings, Raymond, Canada Dept. Mines, Geol. Sur., Mus. Bull. 31, pp. 3-4, pl. 2, figs. 5-7.
- 1946. *Amygdalocystites ?radiatus* Billings, Wilson, Canada Dept. Mines Res., Geol. Sur. Bull. 4, pp. 10-11, pl. 1, figs. 3-4.
- 1950. *?Billingsocystis invaginata* Bassler, Washington Acad. Sci., Jour., vol. 40, No. 9, p. 274, p. 275, fig. 17.

Diagnosis. — Plates with non-expanding rays extending from reduced central boss to plate corners; inter-ray areas pustulose; central boss only slightly elevated.

Range. — Middle Ordovician, Trentonian; Cobourg Limestone?, Ottawa, Ontario; Hull Formation, Healy Falls, Ontario.

Description. — This poorly known species is represented by few specimens, all of which are incomplete or weathered. The species is identified primarily, as indicated in the diagnosis, by the plate prosopon.

The thecal plates are similar to those in *A. florealis* except that the principal rays extending to the corners of each plate do not expand and the central boss is somewhat reduced. Between the rays is a well-developed, pustulose prosopon. No prosoponal ridges are present in the inter-ray areas. On the holotype, larger plates are frequently septagonal and have seven radiating ridges. Smaller pentagonal plates are not uncommon.

The pores are on each side of the prosopon rays and the pair of pores on each facet are situated near the plate corners.

In all other respects, this species resembles *A. florealis*.

Discussion. — There is extant only one known specimen of this species, the weathered holotype (Pl. 5, fig. 7) which is flattened and distally incomplete. There is no sign of the arms, hydropore, gonopore or periproct. The column is partly preserved but shows no evidence of the typical proximal bend.

Raymond (1921, pl. 2, figs. 5-7) included three specimens in this species. However, the plates of his specimens are so weathered that definite assignment to this or the type species of the genus is impossible. Raymond's (*op. cit.*) specimens contain some pinnules which are essentially the same as those in *A. florealis*.

Wilson (1946, pp. 10-11, pl. 1, figs. 3-4) included some plates in *A. radiatus* but, on the basis of her understanding of the sutural pores, was not sure that they were placed in the proper genus. As now understood, these plates are correctly placed and do not belong to *Comarocystites*, as she suggested they might.

Bassler (1950, pp. 274, 275, fig. 17) named a new genus and species *Billingsocystis invaginata*, based on a single, poorly preserved specimen. The plate prosopon is similar to that of *A. radiatus* and may be conspecific with it. The specimen is reported to be "Lower Trenton (probably Curdsville member) on the Versailles and Troy Pike in Woodford County, Kentucky."

Genus **OKLAHOMACYSTIS**, new genus

Type-species: *Amygdalocystites tribrachiatus* Bassler, 1943.

Diagnosis. — Theca globose, inflated; thecal prosopon composed of rosettes of raised triact-ridges; left arm bifurcates with branch extending over anterior face; periproct on anterior face.

Range. — Middle Ordovician, Blackriverian; top of Bromide Formation (Mountain Lake Member) south side of Arbuckle Mountains, Oklahoma. Bassler (1943, p. 696) gave the following localities: "The type is from Sec. 22, T.25S, R.3E, while other localities are SW $\frac{1}{4}$, Sec.3, T.2S, R.3E; and Sec. 14, T.6N, R.16W." The second locality mentioned by Bassler (Sec. 3) is the Buckhorn Ranch locality which has yielded numerous specimens. They are from the upper echinoderm zone, which is about one foot thick, 70 feet below the base of the Viola Limestone (Fay and Graffham, 1969, pp. 37-42).

Description. — The theca is oval to nearly subcircular in profile and usually only slightly compressed into a transversely oval cross section. Generally the anterior face is more protuberant than the slightly flattened posterior face.

The theca consists of 30 to *c.* 95 plates, observed in specimens ranging from 9.5 to 25 mm high. There is no observed relationship

between thecal size and plate number. Intensive intercalation of plates must occur in early juveniles, but ample evidence is present that intercalation continues throughout ontogeny, albeit at a slower rate. Most intercalates occur, in common with other paracrinoids, above the basals on the right side of the theca. The right side of the theca exhibits the common paracrinoid trait of being more protuberant than the left, and is composed of more and smaller plates than the rest of the theca. No plate order is apparent and only the basals, peristomal series, and at least part of the periproctal series can be homologized.

The centers of the plates are solid, slightly concave to slightly convex, and in larger specimens where individual plates have reached large size (*c.* one-half to three-quarters of a centimeter in diameter) the area is pustulose (Pl. 6, fig. 13).

Thecal plates range from regularly to irregularly quadrilaterals to nonagons, the most common shape being hexagonal. Insipient intercalates are quadrilateral or pentagonal, and large, ontogenetically older plates are frequently septagonal, octagonal or nonagonal. Sharply raised, keeled, distally expanding rays extend from the non-porous central area of each plate to the plate corners. At each plate corner is the junction of two other plates. As a result the rays at the juncture of three plates collectively form raised triacts or trigonal pyramids. The resulting pattern is of raised rosettes of four to nine "rays," depending on the number of plate angles (see Pl. 6, figs. 4, 6, 11, 12).

Internally opening pore slits cross most thecal plate sutures. As in *Amygdalocystites*, only two transverse slits cross each suture (Pl. 6, figs. 8, 10). In eroded specimens the paired slits near the internal surface of the plate are closely spaced and lie in between the raised trigonal pyramids. Extending outward through the thickness of the plate, each slit comes to thinly underlie the face of the adjacent raised pyramid. Thus, in cross section the diverging pair of slits forms a V-shaped pattern. Each triact or pyramid has a pore slit on each face which is completely closed to the exterior. [Presumed gaseous exchange would have occurred *via* the stromal tissues traversing the thin "epistereom" coverings of the slits.] There is no evidence for internal connection between the slits along the sides or near the tops of the pyramids.

Growth of the paired slits is presumedly from a single medial pore which subdivides during ontogeny. This is evidenced by what seem to be single pores on small plates (usually in juvenile specimens) and is similar to the condition mentioned above for the specimen of *Ottawacystites* assigned to *A. florealis*. During growth the width of the slits, except in early ontogenetic stages, appears to remain fairly constant. The pair of slits, including the wall between them near the inner surface of the plate, ranges from 0.5 to 1.0 mm in width. As the plates grow, the non-pored central part of the plate expands, which indicates that the juvenile parts of the pore or slit structures are filled in by stereom. This would explain why the probable single pore condition is rarely seen except in the juvenile plate or incipient intercalate.

As is typical in the Paracrinoidea, there are four peristomal plates. The anterior peristomal is pentagonal and comprises most of the anterior part of the opening. Likewise, the posterior peristomal comprises most of the posterior part of the peristome but is larger and irregularly hexagonal in shape. The frustum-like gonopore is centrally situated on this plate. The lateral peristomals comprise only the sharply rounded ends of the transversely oval peristome. The left peristomal is heptagonal to octagonal. The food groove immediately past the peristome splits on this plate and extends into the left lateral and anterior recumbent arms (Pl. 6, figs. 5, 7, 13). The irregularly hexagonal right lateral peristomal joins with the posterior peristomal and another thecal plate to form the raised hydropore slit at their common juncture (Pl. 6, fig. 7). Except at their distal ends where peristomals suture with other thecal plates, these plates generally lack sutural pores. The peristome is only slightly offset from the distal apex, typically to a lesser degree than in *Amygdalocystites*.

The periproct is subapical, closely adjacent to the right arm and invariably on the anterior face. There are four slightly modified thecal plates in the periproctal series. While these plates vary in outline and position, they are probably homologous within the genus. The thecal plate, which joins with the posterior and right lateral peristomals to form the hydropore slit, extends under the right arm and forms the posterior left part of the periproct. The fixed position of this plate assures the fixed position of the periproct and, in all

probability, the homology of the other three periproctals. The margin of the periproct is sharply upturned into a thin, rounded lip. Periproct covering plates are unknown but were doubtlessly present.

The hydropore, which is typically closely juxtaposed to the gonopore, stands in high relief and parallels the right arm (Pl. 6, figs. 5, 7, 13). The tripartite nature of this structure resembles that of the raised trigonal pyramids, and the possibility does exist that the hydropore is a modified sutural pore(s) that opens to the exterior. This possibility exists for other paracrinoid hydropores as well and, if true, would argue for paracrinoids with sutural pores or slits (Comarocystida) to be ancestral to those without them (Platycystitida).

In some larger specimens (18 mm high or more), an anomalous frustum-like pore is found in the central area of a thecal plate (Pl. 6, figs. 4, 5, 12). Generally the pore is on the posterior face, on the first or second plate proximal to the periproct. Other posterior and anterior locations have been noted. The morphology and location of the pore is similar to the anomalous pore in *Sinclairocystis*. It is less frequently developed, however, in *Oklahomacystis* than in *Sinclairocystis*.

The three basals are subequal and typically are offset to the left. The anterior and posterior basals make up most of the column lumen perimeter, while the right basal is restricted to the right side of the transversely oval lumen. The attachment surface for the column is larger on the right basal and is deeper and more roundly excavated into the plate than it is on the other basals. Sutures between the basals lack sutural slits but are normally developed where they suture with thecal plates. The column is unknown.

Oklahomacystis is characterized by the presence of three recumbent arms. The transverse left arm bifurcates adjacent to the peristome and sends the branch across the anterior face. Preservation of the existing material did not favor that of the arms. The right and left arms in mature specimens average 15 or 16 ossicles in composition, while the anterior arm averages about 14 ossicles. Overall, the composition of the arms is similar to that of *Amygdalocystites*, except that the arms have a lower profile. The edges of the concavely excavated underlying calluses rarely extend more than one-half millimeter above the general plate surface, while the middle may

actually be slightly below (Pl. 6, figs. 6, 8, 11). The overall result is a low arm profile. Typically, the primary ossicle is greatly enlarged on the right and left arms, but to a much lesser degree on the anterior arm (Pl. 6, figs. 5, 7, 13). The pinnules are unknown and the covering plates, so far as understood from a single specimen, closely resemble those of *Amygdalocystites*.

The central lumen is limited in its extent. It is best developed in the left arm where it extends nearly to the end of the fourth ossicle. It is double-pronged in the first and second ossicle (similar to *Platycystites*), becoming oval in the distal two. Two lumen is floored by the callus, except where it opens to the interior of the theca *via* a pore under the primary ossicle.

In the right arm the lumen does not extend past the third ossicle and is oval in cross-section throughout. It, too, opens to the interior of the theca under the primary ossicle. The anterior arm is without a lumen.

The arms extend varying lengths down the theca with varying degrees of curvature to the right. Curvature is usually greatest near the distal ends (Pl. 6, figs. 4, 6, 8, 11). The left and right arms may extend nearly to the column attachment and then curve sharply upwards. Typically, however, they extend about two-thirds the distance down the theca. Any of the arms may curve sharply along its length, generally on the upper thecal surface, but curvature is most common with the anterior arm. The anterior arm can, in fact, curve around and intersect the right arm.

Discussion. — Bassler (1943, pp. 695-696) originally assigned this genus as a species of *Amygdalocystites*, presumably because of the overall superficial similarity to it and the presence of transutural pores or slits. *Oklahomacystis* and *Amygdalocystites* have only two slits across each suture, but their disposition through the plates is peculiar to each genus. The depressed centers of the thecal plates, slightly raised sutures (exclusive of the trigonal pyramids) and anomalous pores suggest affinities with *Sinclairocystis* which is found in the same stratigraphic unit. *Oklahomacystis* is sharply distinct from both of the other genera but the obvious similarities bespeak close phylogenetic relationships.

The right and left arms, with their albeit poorly developed arm lumens and large primary pinnules, also attest to their phylogenetic

closeness and homeomorphy. The anterior arm, which lacks a lumen and large primary pinnule base, is probably a secondary feature derived from an ancestor with two recumbent arms, and not from a three-armed form with exothecal arms. In addition, the presence of the complex sutural slit system, anterior periproct and incised arm calluses further suggests that it is a specialized genus in the Comarocystitida.

Oklahomacystis tribrachiatus (Bassler)

Pl. 6, figs. 1-13

1943. *Amygdalocystites tribrachiatus* Bassler, American Jour. Sci., vol. 241, No. 11, pp. 695-696, pl. 1, figs. 14, 15.

The diagnosis, range, and description of this species are the same as given for the genus above.

Order PLATYCYSTITIDA, new order

[Suborder Varicata Jaekel, 1900 (*pars*); Malocystidae Jaekel, 1900 (*pars*); *non* Malocystidae Bather, 1900; Malacocystidae Zittel, 1903 (*pro* Malocystidae Jaekel) (*pars*); Malocystitidae Bassler, 1943 (*pars*)]

Diagnosis. — Paracrinoids without sutural pores; arms epithecal, typically branched; thecal plates generally smooth with pustulose prosopon.

This seems to be the more specialized of the two paracrinoid orders proposed herein. The sutural pores characteristics of the thicker plated Comarocystitida are totally lacking in this order and are presumed to be secondarily lost. More advanced or specialized genera (Malocystitidae) have varying numbers of branched arms.

Canadocystis displays a number of primitive traits relative to other platycystitid genera and morphologically is probably the closest genus to the ordinal radical. It has fairly numerous plates and grows by intercalation of new plates, whereas in most platycystitids the plates are added early in ontogeny, resulting in a rather poor correlation between thecal size and plate number. Also, the arm in some specimens of *Canadocystis* seem to have been distally exothecal, which is a primitive trait.

Platycystites is closely related to *Canadocystis*, as evidenced by the arms. There is a strong resemblance between this genus and the pored *Amygdalocystites*. The similarity is probably due to convergence in adapting to similar paleoecological settings.

Wellerocystis and *Malocystites* appear to be the most specialized genera in the order. Relative to their adult size, their plate numbers are somewhat reduced and the plates themselves tend to be more equidimensional. The branched epithecal arms vary in number and length in *Wellerocystis*. In *Malocystites* the pinnules are recumbent and are deeply impressed into the thecal calluses.

Most platycystitid genera have a fine to coarse pustulose prosopon. Prosopon is usually best developed on the upper (dorsal) part of the theca.

The following genera and families are included in the Platycystitida:

Families	Genera
Platycystitidae, new	<i>Platycystites</i> S. A. Miller, 1889 <i>Canadocystis</i> Jaekel, 1900 = <i>Sigmacystis</i> Hudson, 1911
Malocystitidae Bather, 1899	<i>Wellerocystis</i> Foerste, 1920 <i>Malocystites</i> E. Billings (<i>in</i> Chapman), 1857

Family **PLATYCYSTITIDAE**, new family

Diagnosis.—Ovoid to amygdaloid-shaped thecae (theca with approximately 27 identifiable plates in juvenile specimens); with a pair of transverse, primarily epithecal arms.

Discussion.—This is the only family in the paracrinoids in which most of the plates, especially in juvenile and immature forms, can be homologized. *Platycystites* and *Canadocystis* are relatively simple, more generalized than the genera that make up the Malocystitidae. This family, like the Malocystitidae, is found exclusively in North America.

Genus **PLATYCYSTITES** S. A. Miller, 1889

Type-species: *Platycystites faberi* S. A. Miller, 1889.

- 1889. *Platycystites* Miller, North American Geology and Paleontology, p. 272.
- 1900. *Platycystis* Miller, Bather, Treatise on Zoology, Part III, Echinodermata, p. 51.
- 1911. *Platycystis* Miller, Kirk, U.S. Nat. Mus. Proc., vol. 41, p. 19.
- 1913. *Platycystites* Miller, Bather, Roy. Soc. Edinburgh, Trans., vol. 49, pt. 2, No. 6, p. 371.
- 1913. *Anomalocystites* Hall, Springer, in Text-Book of Paleontology, Zittel-Eastman, vol. 1, p. 150.
- 1943. *Platycystites* Miller, Bassler, American Jour. Sci., vol. 241, pp. 696, 697.

1945. *Platycystites* Miller, Regnéll, Lunds Geol. Min. Inst., Medd., No. 108, p. 39.
1945. *Platycystites* Miller, Sinclair, American Mid. Nat., vol. 34, No. 3, p. 707.
1968. *Platycystites* Miller, Kesling, Treatise on Invertebrate Paleontology, Part S, p. 288.

Range. — Middle Ordovician Chazyan?, Blackriverian, Bromide Formation, Criner Hills and Arbuckle Mountains, Oklahoma; Blackriverian, Ottosee-Benbolt (including ?Heiskell Shale-Holotype), Virginia and Tennessee.

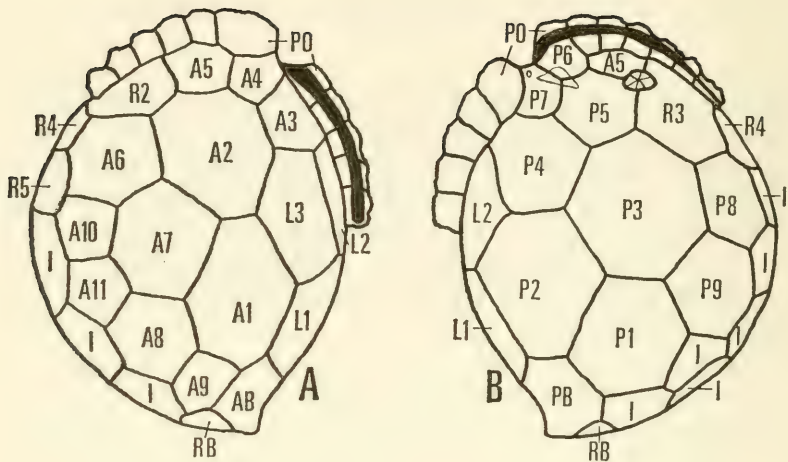
Diagnosis. — Theca amygdaloidal, compressed to broadly oval and inflated in cross section, 27 to 29 identifiable plates with additional intercalates along right lateral margin; maximum number of plates *c.* 47. Peristome usually only slightly offset to left, periproct on posterior face near upper margin. Two epithelial arms which extend varying distances along the lateral margins.

Description. — The theca varies from being amygdaloidal in anterior-posterior profile, as in the type species, *P. faberi*, usually with a depressed oval cross section (Pl. 7, figs. 1-5) to nearly circular in profile, with a broadly oval cross section in many specimens of *P. cristatus* (Pl. 7, figs. 6-15; Pl. 9, figs. 1-14). Some specimens of *P. faberi* are also nearly circular in cross section. It may well be that cross-sectional tumidness may be an environmental response, *i.e.*, perhaps individuals living in more turbulent waters are more compressed to give them more stability. The degree of inflation does not have a strong effect on the profile, therefore, the two species recognized herein can, to a greater or lesser degree, be identified by profile.

There is little change in thecal shape in ontogeny in the type species, while in *P. cristatus* there is a moderate change from oval to more rounded outlines (Text-fig. 4). This is due to intercalation of plates on the right margin and peripheral enlargement of plates in the ambital area (Pl. 8, figs. 4-6).

In the type species, specimens are known to exceed 35 mm in thecal height, while in *P. cristatus* specimens greater than 45 mm high have been observed.

The peristome is canted to the left, as in some other paracrinoid genera. The column attachment in *P. cristatus* is considerably offset to the left, while in the type specimen the attachment is located at the ventral apex of the theca.



Text-fig. 3. *Platicystites cristatus* Bassler. Diagram of the thecal plates and their nomenclature (Pl. 7, figs. 12, 13). *A*, anterior face; *B*, posterior face. *A* (prefix), anterior plates; *AB*, anterior basal; *I*, intercalated plate; *L* (prefix), left plate; *P* (prefix), posterior plate; *PB*, posterior basal; *PO*, primary ossicle of a recumbent arm; *R* (prefix), right plates; *RB*, right basal.

Most of the thecal plates are in more or less fixed positions and readily identifiable from specimen to specimen. Outlines of many of the plates may vary considerably among individuals, but their relative size and relationships to juxtaposed plates is relatively fixed. Plate terminology closely follows that used in *Canadocystis* and plates with the same terminology are assumed to be homologous. Plates with the prefix *A* are entirely or predominantly on the anterior face, the same being true with plates with the prefix *P* on the posterior face. Plates with *L* and *R* prefixes are primarily on the left and right margins respectively (see Text-fig. 3). In some cases, such as *L3* and *R3*, which are on the anterior and posterior faces respectively, the terminology is retained because of the assumed homology of the same plates in the more primitive genus *Canadocystis* (see Text-fig. 7).

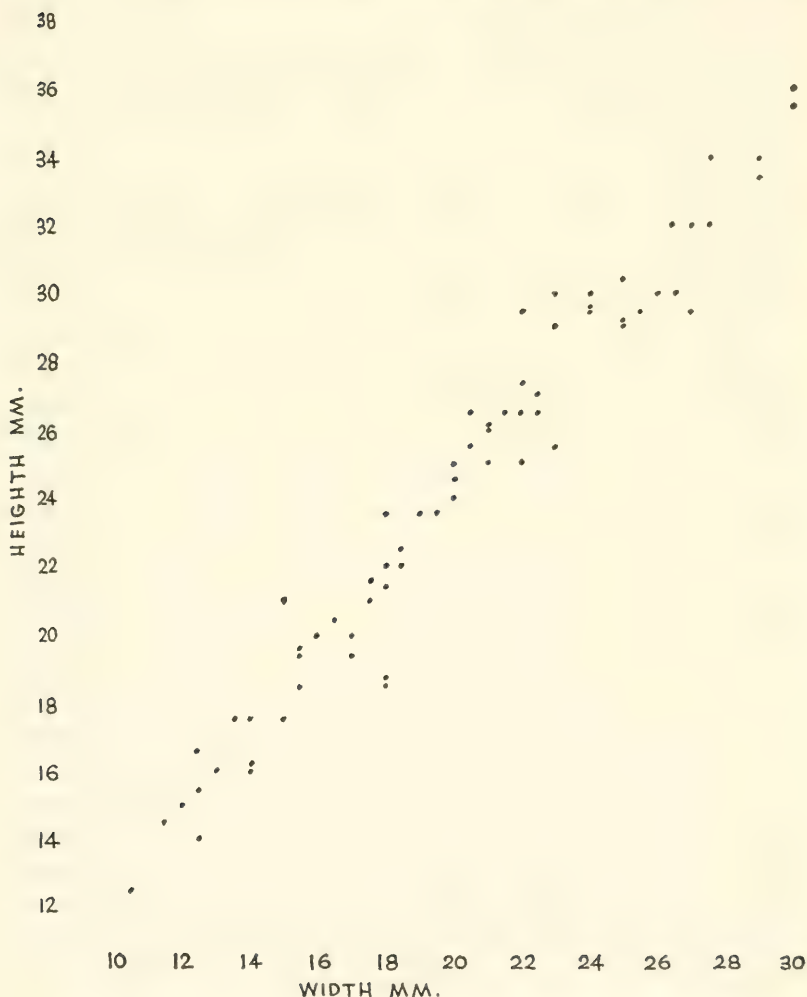
The total number of plates varies to some degree with the species. *P. faberi* has approximately 27 identifiable plates, while *P. cristatus* has 29, but the latter almost always has a number of intercalates, some regularly identifiable along the right side. Intercalation of plates, especially in *P. cristatus*, occurs early in ontogeny and there is little relationship between thecal height and plate number, as there is in *Canadocystis* (Text-figs. 4 and 8).

The three basals, anterior, posterior, and right basals, are somewhat similar to those in *Canadocystis*. *AB* and *PB* are developed on

the anterior and posterior faces and suture on the left margin. They are essentially equal in size, irregularly hexagonal, and together make up most of the column attachment surface.

The right basal *RB* is sharply reduced in size, short, and makes up slightly less than one-third of the column attachment surface.

Above the juncture of *AB* and *PB* is *LI* which extends a short distance between the previously named plates (Text-fig. 3A). It is



Text-fig. 4. Scatter diagram of dimensions of *Platycystites cristatus* Bassler. Growth pattern is uniform throughout ontogeny and results in little change in profile.

sharply geniculated and is narrowly present on the posterior face, but is mainly developed on the anterior face. In outline the plate is irregularly hexagonal, despite its sharp geniculation (Pl. 8, figs. 6, 12; Pl. 9, fig. 8). In *Canadocystis* this plate is paired on the left side with *P2*. Adjacent to *L1* on the anterior face, and in contact with *AB*, is *A1* (Pl. 9, figs. 6, 9). This plate is usually heptagonal and is also generally in contact with *L3*, *A2*, *A7* and *A8/A9*. It usually is the largest plate on the anterior face and generally extends into the upper half of the theca.

Directly above *A1* and *L1* is *L3* which is entirely developed on the anterior face. *L2*, which is primarily on the posterior face, sharply geniculates like *L1* and is narrowly present on the anterior face. *L3* is usually pentagonal and also adjoins *A2* and *A3*.

A2 is located in the mid-upper half of the theca. It is irregularly octagonal, adjoining *A1*, *L3*, *A3*, *A4*, *A5*, *R2*, *A6* and *A7*. The regular outline and position of this plate greatly aids in the identification of other recognized plates (Pl. 8, fig. 9; Pl. 9, fig. 1).

To the right of *A2* is *A6*, an irregularly hexagonal plate that also sutures with *R2*, *A7* and other unnamed intercalates in *P. cristatus* or what appears to be *P8* in *P. faberi*. *A7* and *A8* are to the right of *A1*, both are generally irregularly hexagonal (Pl. 8, fig. 7; Pl. 9, fig. 1). In *P. faberi* these plates are marginal, while in *P. cristatus* they are only slightly right of center, due to the increased number of right side intercalates. Plate *A9* is adjacent to *AB*, *A1* and *A8* in *P. cristatus*. Its position in *P. faberi* is, in part, occupied by *A8* and may be in part homologous with *A8* in *P. cristatus* or a separate, regularized, ?intercalated entity.

The dorsal margin of the anterior face is made up of four plates: *A3*, *A4*, *A5* and *R2* (Pl. 9, fig. 9). *A3* is pentagonal, adjoining *L2*, *L2*, *A4* and *P7* from the posterior face. The dorsal suture is under the recumbent arm. The upper left corner of the plate forms part of the peristome. *A4* is a small plate, quadrate, and sutures with *A2*, *A3*, *A5* and *P5* on the posterior face. It makes up most of the anterior part of the transversely oval peristome. *A5* is irregularly pentagonal, generally extending slightly onto the posterior face where it adjoins *P5*, *P6* and *R2*. On the anterior face it is in contact with *A4*, *A2* and *R2*.

R2 is pentagonal or hexagonal, varying somewhat with species, and extends onto the posterior face where it is in contact with *A5* and *R3*. *R2* and *A5* form the upper margin of the periproct.

In some large specimens of *P. cristatus*, *A9* and *A10* are located on the right side of the anterior face. However, the diagnostic generic plating is limited, as it is on the posterior face, to the left and central parts of the face.

Plates on the posterior face are generally more regular and larger than the anterior face plates (Text-fig. 3B). A notable exception to this are the two small plates *P6* and *P7* which are associated with the hydropore-gonopore and peristome openings.

P1, like *A1*, is located just above *PB* in the basal series (Pl. 9, fig. 10). In *P. faberi* it is in contact with *RB*, while in the more bulbous *P. cristatus* the essentially hexagonal plate *P10* intercalates between and completely separates the two. In addition, *P1* adjoins *P2*, *P3*, *P8* and *P9* on the left, dorsal left, dorsal right and right, respectively. The dorsal extremity of *P1* extends to approximately the midheight of the theca.

P2 is located to the left of, and is slightly larger than, *P1*. Along its left margin it sutures with *L1* which very narrowly extends onto the posterior face. *P2* also adjoins *PB*, *P4*, *P3* and *L2*.

P3 partly intrudes between *P1* and *P2* and is located slightly to the left of center, mostly on the dorsal half of the theca. It also adjoins *P4*, *P5*, *R3* and *P8*.

P4 is located to the left of *P3* and forms a short segment of the left margin in some species of *P. cristatus*. In *P. faberi* and many specimens of *P. cristatus* this (usually) pentagonal plate does not attain the margin, the margin in this area being formed by *L2* and *P7*.

The generally pentagonal *L2* is directly above *L1* and bounded on the anterior face by *L3* and *A3*, and on the posterior face, where it is best developed, by *P2*, *P4* and *P7*.

P8 and *P9* occupy the same positions on the posterior face as *A6* to *A9* do on the anterior (Pl. 8, fig. 10). In the holotype of *P. faberi* they are marginal and suture directly with anterior face plates along the right margin. In other specimens, and in *P. cristatus*, other right side intercalates separate these plates from contact with

anterior face plates. Their shapes, and to some degree their positions, vary, depending upon the amount of intercalation.

The posterior dorsal marginal area is made up of *P5*, *P6*, *P7* and *R3* (Pl. 7, fig. 13). *P5* is generally a hexagonal plate but is modified in that the upper right "angle" forms the lower left part of the periproct. At the upper left angle, which is the juncture for *P6* and *P7*, is the elevated hydropore which is equally shared by all three plates. At its dorsal margin it sutures with *P6* and *A5* which extend across the dorsal margin and narrowly onto the posterior face. *P6* is a small, more or less hexagonal plate, partly between *P5* and *P7*. It forms part of the right posterior peristome opening and sutures with *A4* which forms the right anterior part of the peristomal opening. *P7* is a small, irregularly hexagonal plate which forms most of the posterior and the left posterior part of the peristome opening. *P6* and *P7*, while forming the margin, do not seem to form any significant part of the adjacent food groove leading to the transversely oval opening. This is done by the anterior face plates, notably *A3* and *A4*. Near the peristome lip on *P7* the low rimmed gonopore opens to the exterior.

In *P. cristatus* other plates along the right margin are identifiable, notably *R4* and *R5*. Both plates vary in shape due to the juxtaposed, irregular nature of right side intercalates. *R4* and *R5* are consistently identifiable as being those marginal plates directly ventral to *R2* in the margin. Rarely does the right arm extend farther down the theca than past *R5*.

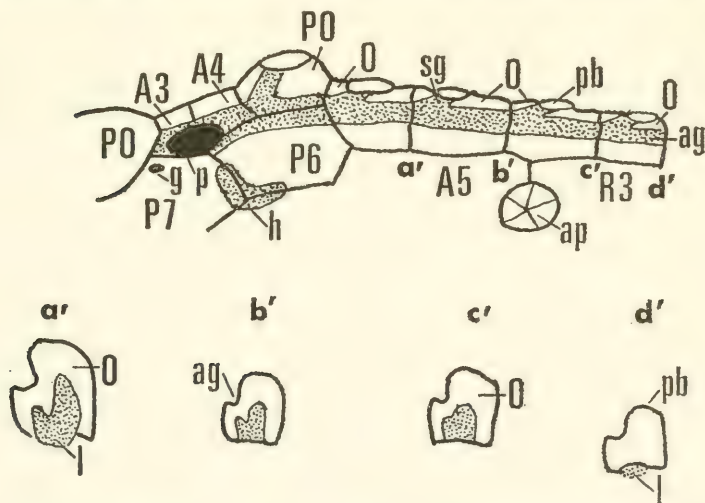
The thecal plates and lateral faces of the recumbent arms are covered with a randomly distributed pustulose prosopon. Prosopon is absent in the flattened to slightly trenched scars, or calluses, on which the recumbent arms rest. These calluses are usually slightly elevated and restricted to the acutely curved lateral margins. Rarely a specimen will display an arm callus which will curve onto either the anterior or posterior face (Pl. 8, fig. 12). Such aberrant growth was probably environmentally controlled.

As indicated above, thecal openings are either on the dorsal margin (peristome) or are located high on the posterior face. Typically, the peristome is offset to the left, transversely oval, and was covered in life by arm covering plates.

The periproct is generally small and was covered by an anal pyramid of eight or nine wedge-shaped plates.

The hydropore-gonopore combination is typical among paracrinoids. The margins of the hydropore are elevated more than in other genera. Other thecal openings under the recumbent arms will be discussed below.

Arms. — The arms, like those of *Amygdalocystites*, are transversely arranged (Pl. 8, fig. 1). In the case of *P. cristatus*, when the peristome is oriented uppermost, the ends of the arms do not extend past a horizontal plane placed at the point where the right arm reaches a vertical position on the theca. Rarely does the right arm pass the vertical when the theca is so oriented that the food groove is overturned and its longitudinal axis is pointed away from the peristome. The left arm, in some instances, extends to the column attachment, and in rare instances extends down the column, as evidenced by arms broken at the column attachment. The extent to which the arm extends down the left side is an intra-species vari-



Text-fig. 5. *Platycystites cristatus* Bassler. Details of the posterior peristomal area and right recumbent arm. Drawings are based on various specimens. *A3*, *A4*, *A5*, *P6*, *P7*, *R3*, thecal plates; *ag*, ambulacral groove; *ap*, anal pyramid; *g*, gonopore located on *P7*; *h*, hydropore located at junction of *P6*, *P7* and another thecal plate; *l*, lumen of the recumbent arm developed between the arm ossicle and thecal callus; *p*, peristome, *pb*, pinnul base; *sg*, sidegroove connecting the food groove on the pinnule to the main ambulacral groove; *a'*-*d'*, transverse views of the recumbent arm at the sutures between the arm ossicles.

ability factor relating to the anterior-posterior ovalness of the theca, *i.e.*, more compressed specimens tend to have relatively longer arms.

In highly compressed forms such as *P. faberi*, the left arm seat extends to the basals, and usually to the column; frequently the right arm also extends to the column attachment, the longitudinal axis of which exceeds the vertical and points away from the peristome when the peristome is oriented uppermost (Pl. 7, figs. 1-5).

The number of arm segments is variable in *P. cristatus*, with a general trend to increase in number with thecal growth. Complete arms are rare and it is not known if a relationship exists between thecal plate numbers and the number of arm segments. The left arm varies between 8 and 16 segments, the right between 5 and 14. Due to the existing data there is, however, no statistical evidence that indicates which arm, on the average, has the greater number of segments. In *P. faberi* the arm segments are poorly known.

As in *Amygdalocystites*, the food grooves open laterally. The connecting grooves to the pinnule bases, pinnule bases, groove covering plates and cross-sectional profile are likewise similar in the two genera (Pl. 8, figs. 1-3).

The pinnule seats on top of the arm plates are subcircular to broadly transversely oval, the outline being interrupted where the pinnule food groove intersects the base. The seat itself is shallowly depressed, often with a bisecting transverse ridge which extends to the pinnule food groove indentation (Pl. 7, figs. 14, 15). No specimen is known with more than one or two pinnule segments intact.

The coelomic canals of the arms are proximally expanded and varied in cross-section; distally they are depressed ovals. Throughout the length of the arms the floors of canals are the thecal plates (Text-fig. 5). No internal connection with the pinnules is present, hence, illustrating an important difference with the Crinoidea.

The expanded portion of the canals is manifest in the proximal four arm plates of the left arm and the proximal six of the right arm. Typically, the canals expand in the central part of each ossicle and constrict towards either end. There is also a slight expansion along the sutures. In these plates with expanded canals, the upper part of the lumen extends upward in two distinct salients: the shorter salient

extends upward under the lateral food groove; the longer upward toward the pinnule base.

The connection between arm lumens and thecal interior occurs proximally under the large proximal arm bases which seat deeply into the theca. In examination of fractured specimens, these deep arm seats are floored with a different colored calcite, which indicates that the plate boundaries are either secondarily extended into the sparry calcite thecal fillings and this part of the arm lumen, now sparry calcite, was open to the interior, or the sparry calcite fillings have altered plate material. Comparison with other genera clearly suggests that the former situation is the case and there were internally opening lumens under the proximal arm ossicles.

The proximal segment of the left arm sits on the "juncture" of *P4*, *P7* and *A3*; the right proximal arm plate on the "juncture" of *P5*, *A4* and *A5*. Between these two deeply incised areas there seems to be (again problematical due to preservation) a canal which passes diagonally through the posterior peristomal plates. Probably there is a connection with the hydropore, and possibly the gonopore as well. Over the periproct there is frequently a depression in the arm callus, and in weathered specimens this depression resembles a pore. Examination of numerous fresh specimens has precluded any direct connection to the interior of the theca at this point.

Column. — The column is similar to that of *Amygdalocystites* in that it is sharply reflexed to the right so that the peristome in life was essentially uppermost (Pl. 8, figs. 1-3).

The column is made up of complete rings, each being externally pustulose. The sutures are distally crenulate, but proximally (at least in *P. cristatus*, the only species of which we have any knowledge of the column) the sutures are so tightly ankylosed that they are not discernible. There is a slight distal tapering in the column and it seems to be especially noticable in the proximal ankylosed part. The distal end of the column is unknown. Within the basals the lumen is transversely oval, but distally in the column it becomes circular in cross section.

Discussion. — Until Bassler's (1943) descriptions of new species from the Bromide of Oklahoma, the published record referred only to the single, poorly preserved holotype specimen of the type species

P. faberi. Its affinities and even its stratigraphic occurrence have been variously discussed in the literature.

S. A. Miller (1889, p. 272) recorded that the holotype "was received by Charles Faber among a lot of fossils from the Kaskaskia Group in the southern part of West Virginia, but as no cystideans have ever been found above the Lower Devonian, and as the specimen is worn as if it had been drifted, the probability is that it belongs to Silurian rocks." Bassler and Moody (1943, p. 180) list the stratigraphic unit as the Heiskell Shale, Scott Co., Virginia. [In Bassler's working copy of this work the unit is emended to read Benbolt-Ottosee, probably on the basis of similar material in the Smithsonian collections from Benbolt-Ottosee outcrops in Virginia and Tennessee.] In all probability the Benbolt is the correct formation which originally contained the holotype.

Bather (1900, p. 51) noted that *Platycystis* (*sic*) "is based on a worn Anomalocystid of indeterminable affinities." Springer (1913, p. 150), in Zittel-Eastman, formally put *Platycystis* (*sic*) in synonymy with *Amygdalocystites* Hall, along with *Ateleocystites* Billings and *Enoploura* Wetherby. The assignment to a "carpoid" group by both was probably based on misinterpretation of S. A. Miller's (*op. cit.*) illustration. Examination of the holotype easily precludes any non-paracrinoid assignment.

Bather (1913, p. 371) modified his position, speculating that *P. faberi* might be a columnar appendage of *Rhipidocystis*, as then understood, "on the nature of the so-called 'basal plates' and their surface of attachment." He further stated that "I do not know on what grounds Dr. Kirk (1911, p. 19) mentions *Platycystis* in connection with *Amygdalocystis*." Kirk (*op. cit.*) probably recognized the close relationship between *Amygdalocystites* and *Platycystites* but did not elaborate on it. Kesling (1968, p. 288) noted that "the curious lack of thecal openings in a completely plated form suggests that Bather's interpretation of it as a columnar appendage of some pelmatozoan may be correct." It is obvious that Kesling was basing his remarks on the original S. A. Miller (*op. cit.*) illustration and not on his examination of the specimen.

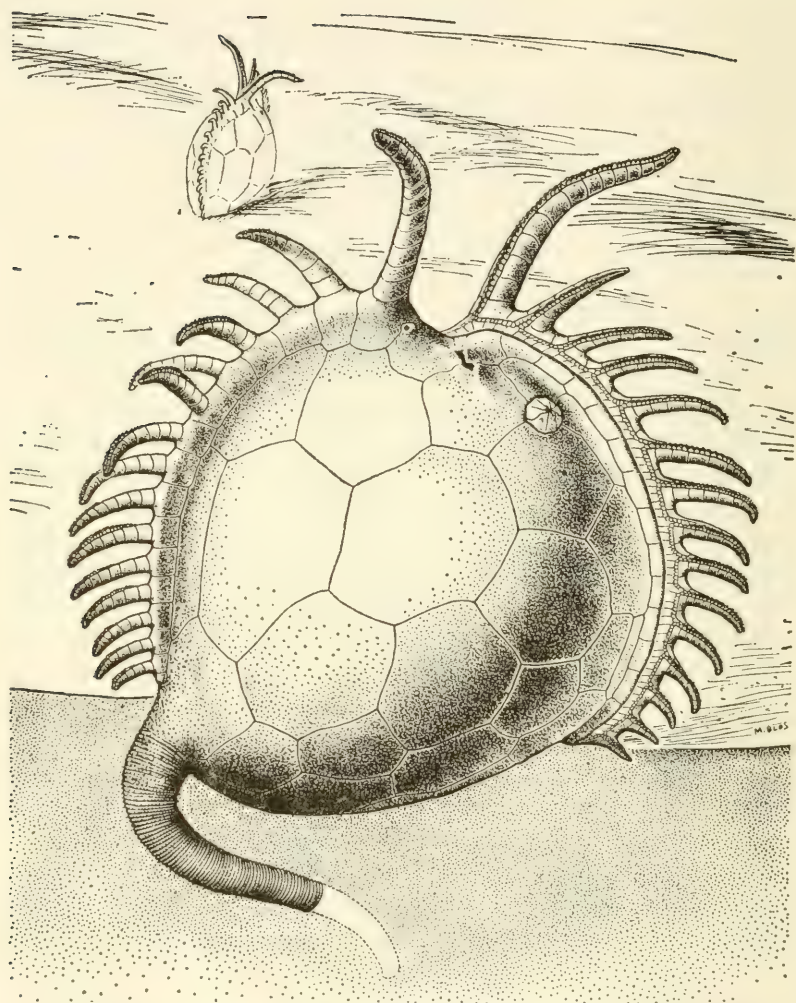
The first new species to be added to the genus was by Bassler (1943, pp. 696-698) who classified them as Malocystitidae. His species are overly typological, being based, for the most part, on

fragments. All of the Oklahoma species can be placed into a single species, *P. cristatus*: this species being selected because it has the best preserved holotype of Bassler's species. Sinclair (1945, pp. 707-709) tentatively emended some of Bassler's descriptions by referring several specimens to his species and added a new species, *P. bassleri*. His material, like Bassler's, is all from the Bromide Formation in Oklahoma and it, too, can be referred to a single species — *P. cristatus*.

Regnéll (1945, p. 39) quoted Bather (1900, p. 51) that the then single, worn specimen was an "Anomalocystid of indeterminable affinities" and made no further mention of this [then] poorly known genus in his work which formally established the Paracrinoidea.

The mode of life was probably similar to that of *Amygdalocystites*: the thecal and arm configuration and curved proximal column attest to this. There is, however, controversy as to what that mode of living was. The authors of this paper have made their position clear above. Professor J. W. Durham, Dept. of Paleontology, University of California, (personal communication) expressed the opinion that the theca is partly buried in the substrate, partly positioned by the sharply curved column which acted as a substrate anchor. He supports his contention by the observation that when the peristome is uppermost the arms terminate in a horizontal plane, presumably at the water sediment interface (Text-fig. 6).

The fact that in the type species the arms extend to the column attachment and, in some cases, probably beyond, and in *P. cristatus* the left arm extends to the column attachment where it is truncated, suggests that the theca was elevated above the substrate on a column. The arms, in some cases, probably extended down the column. The proximally ankylosed column would be an effective way of facing the left side of the theca into prevailing currents, but the probable flexibility distally would allow for the necessary suppleness to preclude breakage. In most specimens the left side is more acutely rounded and the facing of this side into the current would impose the least amount of drag, along with the transversely oriented exothecal pinnules and the column, on the organism. As discussed below, subvective efficiency may have been aided by this orientation.



Text-fig. 6. *Platycystites cristatus* Bassler. Reconstruction of the posterior of the organism. Drawing reflects the opinion of J. Wyatt Durham that this genus lived partly buried in the substrate. (Reconstruction, May Blos, direction of J. W. Durham.)

Platycystites faberi Miller, 1889

Pl. 7, figs. 1-5

1889. *Platycystites faberi* Miller, North American Geology and Paleontology, p. 272.
 1913. *Platycystites faberi* Miller, Bather, Roy. Soc. Edinburgh, Trans., vol. 49, pt. 2, No. 6, p. 371.
 1943. *Platycystites faberi* Miller, Bassler, American Jour. Sci., vol. 241, p. 697.

Range. — According to the original description by S. A. Miller, the holotype was in "a lot of fossils from the Kaskaskia Group [Mississippian] in the southern part of West Virginia; but as no cystideans have ever been found above the Lower Devonian, and as the specimen is worn as if it had been drifted, the probability is that it belongs to the Silurian rocks." Bassler and Moody (1943, p. 180) and Bassler (1943, p. 697) stated that the specimen is from the Heiskell Shale [= Benbolt], Scott County, Virginia. Bassler, in his working copy of Bassler and Moody, modified this to Benbolt-Ottosee, which is probably correct. The label accompanying the specimen from the Walker Museum collection reads "Trenton, Scott County, Virginia."

Other specimens are known from the Ottosee-Benbolt Formations from the following localities. Tennessee: near Luttrell, Evens Ferry, northeast of Washburn, three miles northeast of Bulls Gap, and questionably at the corner of Washington and Spruce Streets in Knoxville, Virginia: on U.S. 19 one and one-half miles southeast of Hansonville, one mile west of Gate City, one-half mile west of Little Moccasin Gap and Rye Cove.

Diagnosis. — Theca in anterior-posterior outline generally amygdaloidal, column attachment at aboral extremity, generally compressed oval in cross-section, but commonly ranges to nearly circular; theca made up of about 30 plates with few intercalated plates along right margin. Arms usually extend to, or nearly to, column.

Description. — The theca tends to be amygdaloidal in anterior-posterior outline. In the holotype and other specimens, the dorsal extremity is sharply rounded, presenting an almost angled appearance. Generally, the more evenly almond to suboval outline is more common. Considerable variation is seen in cross-sectional outline. Compressed oval outlines are apparently more common, but of the known specimens approximately forty percent are clearly

inflated, thus presenting a wide range of variability in this characteristic.¹⁰

There appear to be approximately 30 thecal plates making up the theca, apparently about 27 of which are recognizable in *P. cristatus*, which suggests that limited intercalation along the right side is a species characteristic. A meaningful analysis of the positions and shapes of the thecal plates is not possible at this time.

In almost all cases the column attaches at the aboral extremity of the theca when the peristome is positioned uppermost.

The periproct is relatively larger than in *P. cristatus*. The ventral sutures of *A5* and *R2*, which form the upper half of the periproct, are almost diametrically opposed rather than intersecting at an angle, as is found in the Oklahoma species.

The arms, as evidenced by the arm seats or tracks, extended to, or nearly to, the column. As in *P. cristatus*, the right arm frequently does not extend as far down the theca as the left. In some specimens the seats do not diminish in thickness at the column and it must be inferred that the arms became exothecal at this point or retained their recumbency down the column.

Arm segments are poorly known but appear to be relatively shorter in length and of greater height than those in *P. cristatus*. The arms probably had more segments, hence a greater number of pinnules sweeping through the water. The details of arm and pinnule morphology are essentially unknown.

Discussion. — The probable increase in arm segments may well indicate that the pinnules may have been shorter than in *P. cristatus*. In the latter case the longer pinnules would sweep farther from the theca, while shorter, more closely spaced pinnules would sweep more thoroughly. The total subvective area relative to thecal volume would probably be about the same.

Variations in cross-sectional outline may be environmentally controlled. Compressed specimens may have grown in moving currents, while more inflated specimens may reflect quieter water. The fact that the arms often extend to the column strongly argues for attached forms standing off the substrate.

¹⁰New material may indicate that we are dealing with two or more species, but with the poor material available to the authors, it seems advisable to recognize only the one species from the Appalachian area.

Platycystites cristatus Bassler, 1943 Pl. 7, figs. 6-15; Pl. 8, figs. 1-13;
Pl. 9, figs. 1-14; Text-figs. 3-6

1943. *Platycystites cristatus* Bassler, American Jour. Sci., vol. 241, pp. 697-698, pl. 1, fig. 11.
 1943. *Platycystites levatus* Bassler, American Jour. Sci., vol. 241, p. 697, pl. 1, fig. 13.
 1943. *Platycystites fimbriatus* Bassler, American Jour. Sci., vol. 241, p. 698, pl. 1, fig. 12.
 1943. *Platycystites bromidensis* Bassler, American Jour. Sci., vol. 241, p. 698, pl. 1, fig. 10.
 1945. *Platycystites* cf. *bromidensis* Bassler, Sinclair, American Mid. Nat., vol. 34, No. 3, p. 708, pl. 1, fig. 6.
 1945. *Platycystites* cf. *levatus* Bassler, Sinclair, American Mid. Nat., vol. 34, No. 3, p. 708, pl. 1, figs. 7-8.
 1945. *Platycystites bassleri* Sinclair, American Mid. Nat., vol. 34, No. 3, p. 709, figs. 1-5.

Diagnosis. — Theca with an average of 38 plates, usually somewhat inflated, rounded to oval in anterior-posterior profile in mature specimens. Recumbent arms, rarely reaching the column.

Range. — Middle Ordovician, Blackriverian, Mountain Lake Member of the Bromide Formation, Arbuckle Mountains and Criner Hills, Oklahoma.

Description. — The broadly rounded to oval theca is variable in the total number of thecal plates, ranging from 32 to 47, but to a large degree the number is independent of thecal height. The variety in plate number is due to intercalated plates on the right side and their addition apparently occurs at an early ontogenetic stage. Small, well-preserved specimens are not common, but even the two smallest specimens where an accurate plate count could be made, 8.0 and 9.5 mm high, had 37 and 36 plates, respectively (Pl. 7, figs. 6-9). The average number is 38 for all sizes. At least 39 plates (see above) are recognizable, thus under this scheme this species has from two to seventeen intercalates.

In comparison with *P. faberi*, the basals are generally markedly offset to the left, effected by the intercalates on the right margin, giving the theca considerable right-left asymmetry. Frequently the proximal plane, *i.e.*, at the plane of column attachment, is not at the ventral apex of the theca but slightly dorsal to it.

In this species the arms rarely extend to the column, and in the cases when arm segments do, it is invariably the left arm. Because of preservation it is hard to generalize on the number of segments. Left arms are known to range from 8 to 16 segments, right arms from 5

to 14 segments. There is a direct but very general correlation between thecal height and number of segments. There is some suggestion that the rate of arm segment accretions increases faster in mature specimens, *i.e.*, greater than *c.* 28 mm in height. In most cases the arms lie on the margins, but in a few cases the arms will curve onto the anterior or posterior face. In such cases the theca does not modify in shape as in *Sinclairiocyctis*.

In all other respects this species conforms to the generic description above.

Discussion. — Stratigraphically, this species comes primarily from several beds in the Mountain Lake Member of the Bromide Limestone. As pointed out by Fay and Graffham (1969, p. 39) this and other echinoderm species occur "where shale and limestone are about equally developed, especially along edges of bryozoan bioherms." The thickness of strata through which this species sporadically ranges is about 65 feet and, as pointed out above, no detectable morphological differences have been noted. In Bassler's 1943 (*op. cit.*) paper, he thought all his new species, but *P. cristatus*, were from the Cool Creek Formation in the Criner Hills. As pointed out by Sinclair (1945, p. 707) and especially Amsden (1957, p. 23), Bassler was using "Ulrich's usage of Cool Creek" (Amsden, *op. cit.*). The Cool Creek as now used is in the lower Arbuckle Group which underlies the Simpson Group. The proper stratigraphic placement of Bassler's specimens is the lower Bromide Formation (Mountain Lake Member) of the Simpson Group (Cooper, 1956, p. 120).

All Bromide specimens of *Platycystites* are herein assigned to the single species *P. cristatus*. This species is used because its holotype is the most complete and best preserved of Bassler's (1943, *op. cit.*) species. Material described by Sinclair (1945) is also assignable to this single species.

Genus **CANADOCYSTIS** Jaekel, 1900

Type-species: *Malocystites barrandi* E. Billings, 1858 = *M. barrandei* Billings nom. correct, Jaekel, 1900.

- 1857. *Malocystites* Billings, E., in Chapman, Canadian Jour. Sci., Lit. and Hist., n.s., vol. 2, pp. 302-303 (*pars*).
- 1858. *Malocystites* Billings, E., Billings, E., Canada Geol. Sur., Canadian Organic Remains, Dec. 3, pp. 66-68, pl. 7, figs. 2a-d (*pars*).
- 1895. *Malocystites* Billings, Jaekel in Spengel, Deutsche Zool. Gessel., Verh., Jahrevs. 1895, pp. 111-112 (*pars*).

1905. *Malocystites* Billings, Hudson, New York State Mus., Bull. 80, pp. 270-277, pl. 1, figs. 3-7 (*pars*).
 1911. *Sigmacystis* Hudson, New York State Mus., Bull. 149, pp. 254-257.
 1916. *Canadocystis* Jaekel, Foerste, Ottawa Naturalist, vol. 30, pp. 71, 76, 88, 109, 110.
 1945. *Canadocystis* Jaekel, Regnéll, Lunds Geol.-Min. Inst., Medd., No. 108, pp. 38, 39, 40.
 1968. *Canadocystis* Jaekel, Kesling, Treatise on Invertebrate Paleontology, Part S(1), pp. 279, 281; p. 280, fig. 162.

The diagnosis and description of this genus, based on the type species *Malocystites barrandei*, are difficult because of the poorly preserved type material (Pl. 10, figs. 1-4, 12). Other species, *Canadocystis tennesseensis*, n. sp. and *C. emmonsi*, are much better known and appear closely related to the type species. The diagnosis for *C. tennesseensis* probably will prove to be close to that of the type species (when more material for the latter is available).

Range. — Middle Ordovician, Chazy, ?Laval Limestone near Montreal, Quebec; Valcour Limestone, Valcour Island, New York; Lincolnshire Limestone, Eastern Tennessee; Blackriverian, Benbolt, Lenoir and Wardell Formations, Eastern Tennessee.

***Canadocystis barrandei* E. Billings, 1857** Pl. 10, figs. 1-4, 12

(nom. correct, *pro C. barrandi* Jaekel, 1900 p. 675, *non* Kesling, 1968, p. 279)

1857. *Malocystites* Billings, E., in Chapman, Canadian Jour. Sci., Lit. Hist., n.s., vol. 2, pp. 302-303 (*pars*).
 1858. *Malocystites barrandi* Billings, E., Billings, E., Canada Geol. Sur., Canadian Organic Remains, Dec. 3, pp. 67-68, p. 7, figs. 2a-d.
 1900. *Canadocystis barrandei* Billings, Jaekel, Deutsche Geol. Gesell., 2 eit., Bd. 52, Hft. 4, p. 675.
 1905. *Malocystites barrandii* Billings, Hudson, New York State Museum, Bull. 80, p. 271.
 1911. *Malocystites barrandi* Billings, Hudson, New York State Museum, Bull. 149, p. 253.
 1968. *Canadocystis barrandei* Billings, Kesling, Treatise on Invertebrate Paleontology, Part S, pp. 279, 281; p. 280, fig. 162, 1a,b.

Diagnosis and description of this species on the basis of the available (type) material would be of little value. This species appears to differ only to a minor degree from *C. tennesseensis* and *C. emmonsi*, i.e., the theca tends to be more globose, and there is some indication that the arms may be relatively smaller than in the other species. Until better material is available, the diagnosis and description for *C. tennesseensis* will serve as a general guide to this genus.

Range. — Middle Ordovician, Chazy, ?Laval Limestone, near Montreal, Quebec.

Canadocystis tennesseensis, n. sp.

Pl. 11, figs. 1-15; Text-figs. 7, 8

Diagnosis. — Theca with increasing size, varies from fusiform to globose, made up of 21 to over 40 non-pored plates. Peristome offset to left up to 90 degrees relative to vertical axis of column attachment. Two transverse, uniserial, sigmoidally arranged arms deeply set into the theca which directly adjoin thecal plates, five to eight ossicles to each arm; main food groove partly developed on theca plates. Periproct on right side of theca, near distal apex.

Range. — Middle Ordovician, Upper Chazyan, Lincolnshire Limestone, Eastern Tennessee: Blackriverian, Lenoir and Wardell Formations, Eastern Tennessee.

Description. — The discussion will be based on approximately 200 specimens from eastern Tennessee which are Blackriverian in age. These specimens belong to the species *Canadocystis tennesseensis*, n. sp. and are closely related to the type species, *C. barrandei* Billings and to *C. emmonsii* (Hudson). General conclusions reached regarding *C. tennesseensis* probably hold for the other two species. Focusing on this well-represented species facilitates discussion on variability, ontogeny, and mode of plate addition. Other species are represented by few specimens and none of these are juveniles.

As in most paracrinoids, the peristome is offset relative to the column attachment, but in *C. tennesseensis* this is less obvious in young juveniles and in some large adult specimens. The shape of the theca varies throughout ontogeny and this alone could lead to the recognition of more "species" if only a few specimens from one locality are studied (Pl. 11, figs. 1-13).

Juvenile specimens of *C. tennesseensis*, five to seven millimeters high, are generally subfusiform and are usually composed of 21 to 22 thecal plates (Pl. 11, figs. 2, 3, 9-11). In specimens of increasing sizes it becomes progressively more difficult to identify the original plates which make up the basic plate pattern (Text-fig. 6). The original thecal plates above the basals are not arranged into uniform series and vary considerably in size. The peristome generally is only slightly offset in these specimens.

Individuals in the eight to twelve millimeter size range usually alter their shape but only add several thecal plates, the total number of thecal plates averaging 22 to 24. The left side of the theca between

the column attachment and the recumbent arm is only slightly convex, as in smaller juveniles. The right side is protuberant and, typically, the peristome is markedly offset. Variability of the latter trait is considerable, however. Peristomal offset to the left may be slight to nearly 90 degrees with the column axis (Pl. 11, fig. 6). It is quite possible that this variation is, in part, paleoecologically produced.

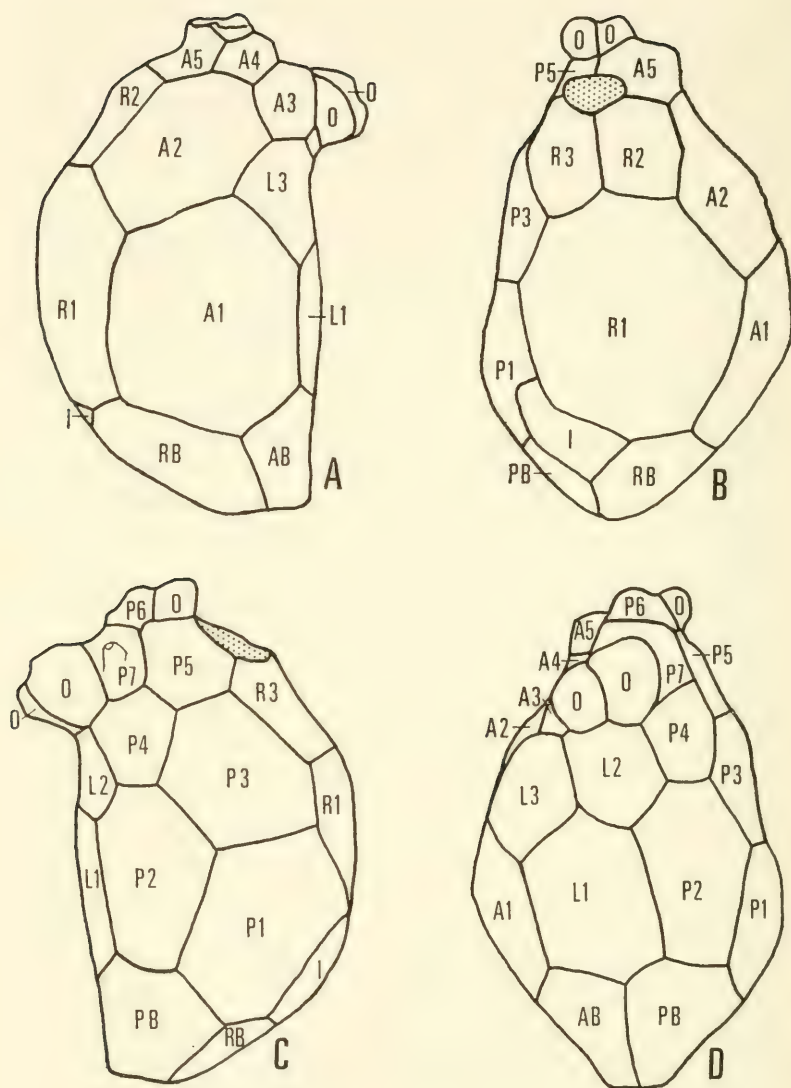
All known extant specimens of *C. emmonsii* are between eight and twelve millimeters high, and the peristomes are sharply offset. They differ in that the theca is composed of 28 to 29 plates. Perhaps the number of thecal plates relative to thecal height is a valid species taxobasis; possibly it is only at certain ontogenetic stages.

Canadocystis tennesseensis specimens 12 to 13 millimeters high begin to develop a more convex left side, resulting in a lessening of the peristomal offset. At this stage the theca begins to assume a more or less circular cross section compared to the more oval outline of smaller specimens (Pl. 11, figs. 1, 6, 7). The rate of plate addition in the theca is unknown above the 12 to 13 millimeter stage, where 24 plates are usually present.

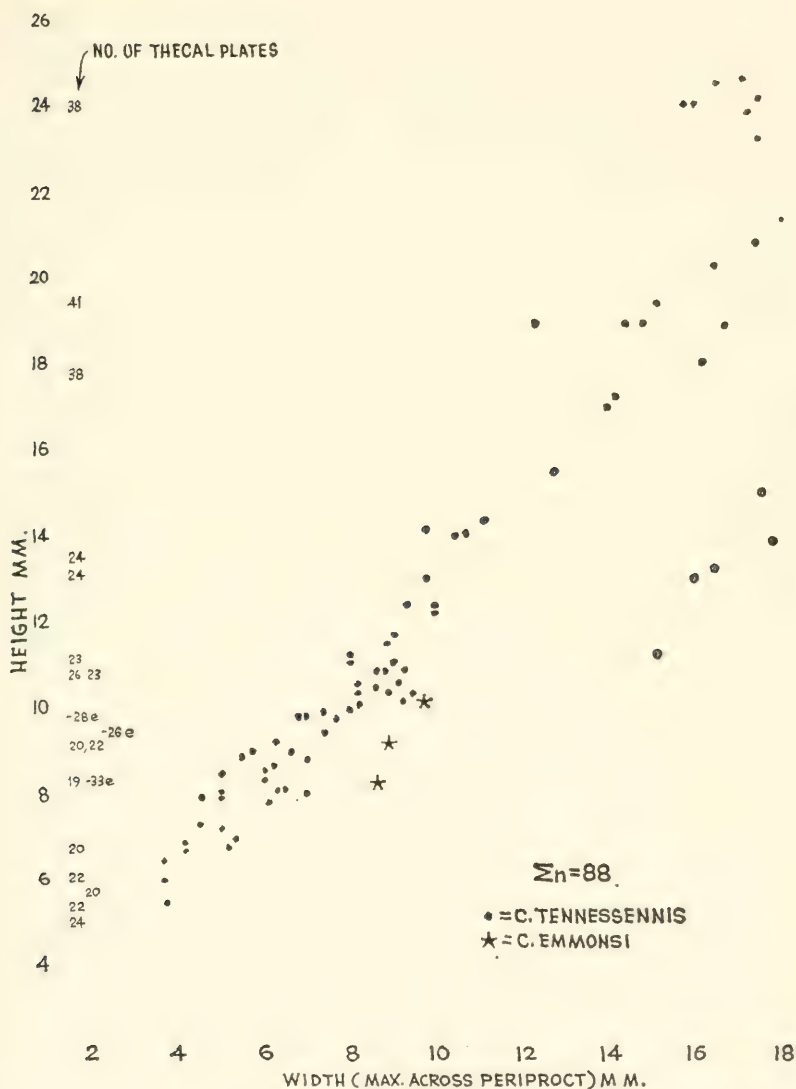
Specimens above 15 millimeters in height generally take on an oval profile, and the peristome is usually only slightly offset.

In individuals of *C. tennesseensis* between 18 and 27 millimeters high, the theca is made up of 38 to 41 plates. Between the heights of 13 and 18 millimeters, there apparently is a stage where 12 to 15 plates are added, but in larger specimens increase in thecal size is primarily due to plate growth (Pl. 11, figs. 12, 13). Unfortunately, this stage of plate addition is not recorded in the available material.

The column attachment, like the peristome, is offset to the left, relative to the bilateral plane of symmetry, in the transverse plane of the theca. The attachment base is formed by the three basal plates which are all nearly equal in height but unequal in width. On the right side, bisected by the transverse plane, is the largest basal. It extends through nearly 180 degrees of the basal circlet in most specimens but may make up slightly less, especially in large individuals (15 millimeters or more in height). The other two basals are smaller and subequal, the anterior plate often being slightly smaller. Their common suture is in the transverse plate on the left side of the theca.



Text-fig. 7. *Canadocystis tennesseensis*, n. sp. Diagram of the thecal plates and their nomenclature (Pl. 11, figs. 9, 10, 11). *A*, anterior face; *B*, right face; *C*, posterior face and *D*, left face. *A* (prefix), anterior plates; *AB*, anterior basal; *I*, intercalated plate; *L* (prefix), left plate; *O*, ossicle of a recumbent arm; *P* (prefix), posterior plate; *PB*, posterior basal; *R* (prefix), right plates; *RB*, right basal. Stippled area is the periproct.



Text-fig. 8. Scatter diagram of dimensions of *Canadocystis* Jackel. There is little relationship between thecal size and the number of thecal plates on specimens under 14 mm in height. Larger specimens, more than 20 mm in height, are elongated relative to thecal width. Numbers of thecal plates with an *e* postscript are specimens of *C. emmonsii*.

Above the basals are five plates which are usually hexagonal, but where adjoining intercalates may have more facets. Moving in a clockwise direction from the anterior face, these plates are as follows: Anterior 1 (*A1*) is over parts of the right and anterior basals (see text-fig. 7). Right 1 (*R1*) is directly above the right basal. Posterior 1 (*P1*) is over parts of the right and posterior basals, and Posterior 2 (*P2*) is directly above the posterior basal. Left 1 (*L1*) is over parts of the anterior and posterior basals.

Above this irregular circlet the plates are identifiable in small specimens but are not arranged in series. Moving clockwise from the anterior face are the following seven plates: Above *A1* is the pentagonal to hexagonal Anterior 2 (*A2*). This plate extends orally only slightly above *R1*. Over *R1* is a pair of essentially pentagonal plates, Right 2 (*R2*) and Right 3 (*R3*). The adoral edges of these plates form the lower margin of the periproct. Superior to *P1* and *P2* are Posterior 3 and 4; the upper edges of both are in contact with the arms and posterior peristomal plates. Posterior 3 is irregularly pentagonal to hexagonal and is situated primarily above *P1*. Posterior 4 is similarly shaped to *P3* and is located primarily above *P2*. Above Left 1 is a pair of pentagonal plates which dorsally are in contact with the left recumbent arm. Left 2 (*L2*) also is in contact with *P2* and *P4*, while Left 3 (*L3*) also sutures with *A1* and *A2*.

On the dorsal extremities of the anterior and posterior faces are six plates (three on each face) of which four (two on each face) are periproctals. On the anterior face these plates are, clockwise, *A3*, *A4* and *A5*. Anterior 3 is fan-shaped and forms part of the main food groove associated with the left recumbent arm, as well as being a peristomal. Anterior 4 is quadrate and a peristomal. Anterior 5 is pentagonal and extends to the periproct where it forms the anterior dorsal fourth of the margin.

The posterior dorsal plates are similar to the three on the anterior face. Posterior 5 (*P5*) is a large pentagonal plate which dorsally is usually covered by the recumbent right arm. Part of this plate's right side forms the upper left quarter of the periproct margin. On Posterior 5's left side it is included in the lower right quarter of the hydropore mound and slit. Above *P5* is Posterior 6 (*P6*) which, like *A3*, is somewhat fan-shaped and forms part of the main food groove of the right recumbent arm. Unlike *A3*, this plate is a

peristomal. Part of the aboral margin of *P6* makes up most of the upper half of the hydropore mound and slit. Posterior 7 (*P7*) appears to be a modified arm plate, but this resemblance is only coincidence. This pentagonal plate bears the gonopore which is elevated on a low frustum. The plate makes up the lower left quarter of the hydropore mound and slit, and forms most of the posterior margin of the peristome.

Plates are added by intercalation subsequent to the basic 21 which make up the juvenile theca. All intercalates apparently originate at the juncture of three plates. There may be exceptions in plates added adjacent to the peristomal series and around the periproct in larger specimens. It is not clearly determined, however, if these latter cases are truly exceptions to the general condition. Intercalated plates in their early stages are triangular with convex sides. With growth, they become rhomboid, and finally they typically assume a regular to irregular hexagonal outline.

In smaller specimens, specific areas are more likely to have intercalates than others. For example, an intercalate commonly occurs between right basal, posterior basal and *P1*. With growth it will also adjoin *P2*. Another common intercalate is above the right basal between *R1* and *A1*. In some cases a second intercalate may form at the same point above the basal after the first intercalate has attained large (hexagonal) size. Above the right basal are frequently several more intercalates, and it is these supra-basal intercalates that significantly cause the marked convexity of the right face in specimens 8 to 12 mm in height.

Other intercalated plates occur over the entire theca, especially in larger species (greater than 12 mm high) but are less numerous on the left face. The basals and peristomal series always remain intact and are never separated by intercalates. There is some indication that unhindered addition of plates takes place under the recumbent arms.

Arms.—The two gently tapering, sigmoidally arranged, recumbent arms [the *sigma* of Hudson (1905, p. 270)] of this genus stand in sharp relief above the theca. The arms, unlike those of other paracrinoid genera, are deeply sutured into the thecal plates (Pl. 11, figs. 5, 14, 15). Calluses underlying the arms are non-existent in this genus. The deep "V" shaped facets of the basal por-

tion of the arm plates do not, however, displace the thecal plates to the extent that they extend into the body cavity. In all cases, arm plates are underlain by thecal plates, albeit the thecal plates are thin, especially near the peristome.

The number of arm ossicles varies from 5 to 11; the right arm usually with one or two more than the left (Pl. 11, fig. 14). Arms attach to the theca along the inside lateral face, as well as the basal face. Arm ossicles are essentially rectangular to keystone-shaped when viewed laterally (outside lateral face). Dorsally, the sutures between the arm ossicles and thecal plates run along the axes of the main food grooves. The main grooves are unusual among paracrinoids in that they are in part formed by thecal plates. Sutures separating arm ossicles are transverse but do not run down the side food grooves. The side food grooves that lead to the pinnule bases occur along the proximal side of the arm plate but are not marginal.

The arm ossicles each bear a pinnule base which is dorso-lateral in position and is connected to the main food groove by a side food groove. On the terminal ossicle the main and side groove are one; the main groove extended onto the terminal pinnule. As new arm ossicles were added part of the penultimate ossicle must have been resorbed and the newly formed portion of the main groove thence extended onto the terminal ossicle. The portion of the food groove on the penultimate and other proximal arm ossicles prior to resorption remains as the side food groove.

The pinnule bases are circular to oblong and depressed. The surface of the base is pustulose, probably providing anchorage for arm to pinnule ligaments. In some cases, *e.g.*, *C. emmonsi*, these attachment bases are more elaborate and appear to be a species characteristic. As in most recumbent-armed paracrinoids, the arm ossicles and pinnule bases adjacent to the peristome are somewhat enlarged. The pinnules are unknown in this genus.

Canadocystis emmonsi (Hudson), 1905

Pl. 10, figs. 5-11

1905. *Malocystites emmonsi* Hudson, New York State Mus., Bull. 80, pp. 270-277, pl. 1, figs. 3-7.
1911. *Sigmacystis emmonsi* (Hudson), Hudson, New York State Mus., Bull. 149, pp. 254-257.
1915. *Canadocystis emmonsi* (Hudson), Bassler, U.S. Nat. Mus., Bull. 92, p. 181.
1916. *Canadocystis emmonsi* (Hudson), Hudson, Ottawa Naturalist, vol. 30, No. 2, pp. 45-46.

1968. *Canadocystis emmonsii* (Hudson), Kesling, Treatise on Invertebrate Paleontology, Part S, pp. 279-280, figs. 162, 2a-g; 163.

Diagnosis. — *Canadocystis* with thickened protuberant primary plates on right, anterior, and posterior faces. Pinnule bases with well-defined ligamental pits.

Range. — Chazy: Middle Chazy Limestone, Valcour Island, New York.

Description. — This species has been described in detail by Hudson (1905, pp. 270-277; 1911, pp. 254-257). There are, however, aspects of morphology that warrant further description and discussion. In many aspects, this species is very similar to *C. tennesseensis*. The differences, however, are easy to discern and diagnose.

Hudson (1905, p. 270) noted that the average number of thecal plates, exclusive of the arm plates, is 43, or over twice as many as the basic 21 in this genus. However, with the three available specimens, the types, the average number is 31. Hudson's figures are derived from some 200 specimens; their whereabouts at present are unknown.

The theca of *C. emmonsii* is relatively thicker (anterior-posterior) and more protuberant on the right side than *C. tennesseensis*. The greater tumidness is due to the greater number of suprabasal intercalates on the right side. Smaller intercalates are also common above the basals on the anterior and posterior faces. The intercalated plates are larger toward the right side of the theca. Triangular and quadrangular intercalates are not uncommon.

The primary plates are greatly thickened and protuberant (umbos of Hudson, 1905) on the right, anterior, and posterior faces. Primaries *A1*, *A2*, *R1* and *P1* are notable in this aspect.

Typically, the peristome is more offset, relative to the vertical column axis, than in *C. tennesseensis*. Because of the few available specimens of *C. emmonsii*, it is impossible to determine if this is a species trait. The figures given by Hudson (1905, p. 270) of a 40 to 80 degree offset from the column axis would seem to indicate, however, that the offset is greater.

In all other aspects of thecal morphology, periproct, pores, this species varies little from *C. tennesseensis*.

The recumbent arms also have essentially the same number of ossicles and overall morphology as in *C. tennesseensis*. There are,

however, marked differences between these species in the nature of the pinnule bases. In *C. tennesseensis* the bases are planar to concave and pitted. Admittedly, this may be a preservational feature. but the nature of the pinnule base seen in *C. emmonsi* is restricted to that species.

On well-preserved arm plates, the circular pinnule base is bounded by an elevated rim which is broken by the excavated side food groove and by a second depression, diametrically opposite the side food groove, extending from the middle of the base to the periphery. The latter depression is incised on a ridge which, like the groove, gently expands away from the side food groove. On either side of the ridge are shallow, half-elliptical to lunate depressions which, like the groove mentioned above, were seats for ligamental attachment. The ridge and outside rim appear to be of equal height; the maximum depth of the ligamental seats seem to be essentially the same in each arm ossicle. The pinnules are unknown.

Discussion.— In the establishing of this species (as *Malocystites emmonsi*) Hudson (1905, pp. 271-277) designated three types: a holotype (his Specimen A) and two paratypes (his Specimens B and C). Hudson (1911) established the genus *Sigmacystis* with *M. emmonsi* as type species. In doing so he designated (erroneously) Specimen C as the type for his new genus. In addition to his violation of the rules of zoological nomenclature, he was apparently unaware of Jaekel's (1900) assignment of *M. barrandei* to *Canadocystis*. Bassler (1915, p. 181) apparently was the first to place *M. emmonsi* = *Sigmacystis emmonsi* in *Canadocystis*, as have most succeeding authors, including Hudson (1916, pp. 45-46) himself. The present study confirms Bassler's assignment.

Hudson (1905, p. 275) mentioned that he examined over 200 specimens in his study, unfortunately only the type material appears to be extant.

Hudson differentiated *M. emmonsi* from *M. barrandei*, in part, on the basis that the ambulacra or "sigma" rests on an attenuated portion of the theca in the former species. This is probably inaccurate because small specimens of *C. tennesseensis* also show this feature. Hence, this is probably more of a size characteristic than a species characteristic. The type specimen of *C. barrandei*, which Hud-

son was comparing with his material, is 25.7 mm high. Large specimens of *C. tennesseensis* (greater than 10 mm in height) are never "necked." In the same vein, Hudson (1905, p. 271) noted (a personal communication from P. E. Raymond) that the recumbent arms are more elevated in *C. emmonsii* than in *C. barrandei*. This is also a size phenomenon; the arms do not appreciably increase in size (at least in *C. tennesseensis*) past the 12-15 mm height stage.

Family **MALOCYSTITIDAE** Bather, 1899

[nom. correct. Bassler, 1938 (*pro* Malocystidae Bather, 1899)]

Diagnosis.—Platycystitids with branched subvective structures which spread over the generally inflated theca (modified from Kesling, 1968, p. 277).

This family contains two genera, *Malocystites* and *Wellerocystis*. While more specialized than the Platycystitidae, this family does not exhibit the somewhat fixed plate pattern seen in them. It is suspected that a fairly fixed pattern is probably present in juvenile malocystitids, but this is disrupted by early intercalation of plates. While both genera have multiple branched subvective structures, the similarity is deceiving. In *Wellerocystis* the recumbent arms have well-defined pinnule bases from which pinnules undoubtedly extended. In *Malocystites* the recumbent "arms" are, in fact, recumbent pinnules, as suggested by Sprinkle (1973, p. 185). The arm pattern itself is somewhat sigmoidal, like that of *Canadocystis*. The general aspect of the theca is similar to that of *Wellerocystis*, while in the strict sense the nature of the arms is more like that of Platycystitidae. The lack of plate order, the inflated theca and reduced hydropore, attest to the probable close relationship of *Wellerocystis* and *Malocystites*.

Genus **MALOCYSTITES** E. Billings, 1857

Type-species: *Malocystites murchisoni* E. Billings, 1858.

- 1857. *Malocystites* Billings, E., in Chapman, Canadian Jour. Sci., Lit. Hist., n.s., vol. 2, pp. 302-303 (*pars*).
- 1858. *Malocystites* Billings, E., Billings, E., Canada Geol. Sur., Canadian Organic Remains, Dec. 3, pp. 66-67, pl. 7, figs. 1a-1i (*pars*).
- 1859. *Malocystites* Billings, Hall, Paleont. New York, vol. 3, p. 152 (*pars*).
- 1879. *Malocystites* Billings, Zittel, Handbuch der Palaeontologie, Bd. 1, p. 413.
- 1889. *Malocystites* Billings, S. A. Miller, North American Geology and Paleontology, p. 259.

1891. Non *Malocystis* Billings, Carpenter, Linn. Soc. Jour.-Zool., vol. 24, p. 50 [= ? "*Holocystites*" *elegans*, S. A. Miller, see Paul, 1971, p. 151].
1895. *Malocystites* Billings, Jaekel, in Spengel, Deutsche Zool. Gesell., Verh., Jahrevs. 1895, pp. 111-112 (*pars*).
1896. (1895) *Malocystis* Billings, Haeckel, Jena Zeit., Bd. 30, p. 401 (*pars*).
1896. *Malocystis* Billings, Haeckel, Die Amphorideen und Cystoideen, fest. Siebenzigsten Geburtsage von Carl Gegenbaur, Bd. 1, pp. 102, 105.
1900. *Malocystis* Billings, Bather, Treatise on Zoology, Ed. E. R. Lankester, Pt. III, Echinodermata, p. 58 (*pars*).
1900. *Malocystites* Billings, Jaekel, Deutsche Geol. Gesell., Zeit., Bd. 52, Hft. 4, pp. 674-675.
1903. *Malacocystites* Billings, Zittel, Grundzuge der Palaontologie, Abt. 1, p. 172.
1905. Non *Malocystites* Billings, Hudson, New York State Mus., Bull. 80, pp. 270-277, pl. 1, figs. 3-7; = *Canadocystis* (*pars*).
1913. *Malocystis* Billings, Springer, in Zittel (Eastman ed.), Text-Book of Paleontology, vol. 1, p. 151.
1916. *Malocystites* Billings, Foerste, Ottawa Naturalist, vol. 30, pp. 109, 110.
1918. *Malocystites* Billings, Jaekel, Pal. Zeit., Bd. 3, p. 27.
1920. *Malocystites* Billings, Foerste, Ohio Jour. Sci., vol. 21, No. 2, p. 38.
1945. *Malocystites* Billings, Regnéll, Lunds Geol.-Min. Inst., Medd., No. 108, p. 39.
1958. *Malocystites* Billings, Gekker, Eesti NSV Teaduste, Geologia Instituudi Uurimused III, pp. 154, 155.
1968. *Malocystites* Billings, Kesling, Treatise on Invertebrate Paleontology, Pt. S, pp. 272, 273, 275-278; 278, fig. 160.
1973. *Malocystites* Billings, Sprinkle, Mus. Comp. Zool., Spec. Pub., pp. 185, 186.
1973. *Malocystites* Billings, Sprinkle, Jour. Paleont., vol. 47, No. 5, p. 870.

Diagnosis. — Theca globose, *c.* 33-58 non-pored plates [thecal plates not more numerous on right side]. Column attachment only slightly offset to the left; two recumbent arms with eight to ten recumbent pinnules deeply imbedded into narrow but prominent calluses. Periproct anterior right lateral near apex.

Range. — Middle Ordovician, Chazy, Chazy Limestone, Isle of Montreal and Laval-des Rapides, Isle of Laval, Quebec; Valcour Limestone, Valcour Island, New York.

Description. — The theca ranges from globose in smaller specimens to broadly oval with a broadly oval to round cross section in larger specimens. The maximum size range is unknown, but the height range of specimens available for this study was 13 to 31 mm. Thecal elongation, relative to width seen in other non-pored paracrinoids, is estimated to have occurred at around 20 mm in height. Only two plate counts have been made on complete specimens; one 33 (?34), on a specimen 12 mm high (Pl. 12, figs. 7, 8, 9); the other 58, on a specimen 16 mm high (Pl. 12, figs. 1-3, 5). In the latter case triangular and quadrangular intercalates are not uncommon.

Intercalated plates are generally found proximal to the ambitus, but contrary to the usual paracrinoid pattern, they are fairly uniform in distribution and do not predominate in the right-lateral area of the theca. The thecal plates above the ambitus, and below, as well, in larger specimens, are hexagonal or pentagonal. They are relatively larger and more equidimensional than in other paracrinoids.

There is some possibility that some of the thecal plates, especially those adjacent to the periproctal and peristomal series, may be uniform in position. The lack of material, and intercalation in larger specimens, precludes this aspect of our investigation.

It appears that there are four peristomal plates. The morphology of these plates is still somewhat problematical. There appear to be anterior and posterior peristomal plates which are irregularly hexagonal. The lateral plates near the peristome are poorly understood due to callus overgrowth. Apparently the right peristomal, in typical paracrinoid fashion, joins with the posterior peristomal and a thecal plate to form the raised hydropore slit, and it also extends anteriorly to form part of the periproct rim. The left peristomal apparently has three or four arm plates on its outer surface. Plate outlines for both lateral peristomals are apparently irregularly hexagonal.

The periproct is invariably located on the anterior face, to the right and slightly ventral to the peristome (Pl. 12, figs. 2, 7, 13). It lies between the transverse right and the right anterior recumbent pinnule. These are four periproctals which appear to be consistent in position. The lower pair are irregularly pentagonal to heptagonal in outline; the higher number of facets is present in larger specimens. Outlines of the upper two periproctals are problematical because the arm calluses mask the sutures.

The basals are subequal and polygonal, the number of facets varying with the number of adjacent intercalates. The basal series is typically offset to the left but is slightly offset posterior to the transverse plane. This contrasts with *Wellerocystis* where the basals are offset to the anterior of the transverse plane. The series is also rotated about 45 degrees to the right (counter-clockwise). This is determined by assigning the basal with the least surface in the make-up of the column lumen as the right basal (*RB*), which is consistent within the paracrinoids, and in this case is rotated from

its usual transverse position (Pl. 12, fig. 5). [The plate assigned as the *RB* also has a large indented area serving as the surface of column attachment, which is also typical.] The surface of column attachment is not well preserved in existing specimens but appears to be slightly undulating due to convexly curved surfaces on the anterior (*AB*) and posterior (*PB*) basals. Outline of the lumen through the basals ranges from circular to broadly oval.

On unweathered surfaces the thecal plates, exclusive of callus material, are covered with concentrically arranged pustulose pro-sopon. Pustule size is fairly uniform over the entire thecal surface and there is no evidence of increase in pustule size toward the periphery of individual plates (Pl. 12, figs. 2, 12).

The hydropore slit is small in comparison with other paracrinoids, although typical in position (see above) (Pl. 12, fig. 2). The gonopore has not been observed, but it is assumed to be typically located on the posterior lip of the peristome. Like the hydropore, it is probably unusually small. There are no observed anomalous pores.

The ambulacra in *Malocystites* are the most evolved in the Paracrinoidea. Both primary arms are four or five segments in length and apparently are on the lateral peristomals. The arm ossicles are sigmoidally arranged, as in *Canadocystis*, and the disposition of the food groove is remarkably similar. The lumen under the arm ossicles appears to be greatly reduced or is missing. Extending from each one of the segments is an epithecal pinnule. The total number of pinnules is eight or ten; unequal numbers of pinnules on opposite arms of an individual have not been observed (Pl. 12, figs. 2, 7, 11, 12, 13). The pinnules on their narrow, but sharply raised, calluses radiate over the thecal surface. Spacing between the pinnules is subequal, with the widest spacing occurring between the anterior right and lateral right pinnules (their inter-area containing the periproct) and the lateral right pinnule and the first right postero-lateral pinnule. The narrowest spacing occurs between the two anteriormost pinnules of the left side and the two posteriormost pinnules on the right side. The presence or absence of these closely spaced pairs on each face is determined by the number of arm ossicles, *i.e.*, four or five in each. At this stage of our knowledge, and with the limited material, it seems prudent to regard this difference in arm

number as simple intraspecies variation. The pinnules in some specimens spiral clockwise and extend aborally almost to the basals. In some specimens pinnules will converge, join and distally diverge. The course of the pinnule is not always straight or gently curving. Irregular bending is not uncommon. There is little to suggest that the pinnules become relatively longer during ontogeny; small specimens may have pinnules reaching almost to the basals. Relative lengthening, if any, must take place in early stages of ontogeny.

The main food groove is shallow and round-bottomed, located on the arm ossicles. It extends distally on top of the pinnules and is not lateral in position. Over the food groove on the arms and pinnules are the biserial covering plates. The plates on the arms, unlike some other genera, are equal in size. They are arranged in an alternating pattern and their irregular suturing above the mid-line of the food groove suggests that the plates were fixed in position, *i.e.*, non-erectile. Covering plates on the pinnules are, likewise, alternating with about two pair for each pinnule ossicle, but sharp zig zag suture between opposing plates clearly indicates erectile plating. The pinnule ossicles are low in profile and deeply impressed into the underlying calluses. Ossicle scars of the pinnules are prominent and the transverse callus walls between the ossicles are as high as, or higher than, the lateral margins of the callus (Pl. 12, fig. 2). The presence of deeply impressed pinnules was probably necessitated by living in a strong current environment (Sprinkle, 1973, p. 879). The lack of pinnule lumens makes the deep inset of the ossicles possible.

Only the proximal part of a single column is known (Pl. 12, fig. 6). Its segments are circular, holomerous, short and with crenulate articulating surfaces. The column has a circular lumen which occupies approximately one-third of the total diameter. There is some evidence that the columnals themselves may be slightly undulating. This would correspond to the apparent undulating attachment surface on the basals. Perhaps the undulatory nature of the columnals and their crenulate articulating surfaces bespeak of a rigid proximal column, which seems to be a general class trait. As in most paracrinoids (especially non-pored Platycystitida), the column is thin, relative to thecal size.

Discussion.—*Malocystites* has been variously assigned to

"cystoid" groups in earlier literature. It has often been discussed (hence the lengthy synonymy), but *Malocystites* remained poorly understood. Early attempts to classify it in lower taxonomic groups, *i.e.*, lower than Class Cystoidea, apparently began with Zittel (1879, p. 413) when he placed it in the family Aporitidae, a catch-all grouping for "cystoids" without thecal pores. Haeckel (1895, pp. 111-112; 1896, p. 401) placed *Malocystites* in the cystoid family Fungocystida, a group containing diploporid cystoids and the paracrinoid *Amygdalocystites*. Bather (1900, p. 58) placed *Malocystites* and *Amygdalocystites* in the family Malocystidae which he included under the order Rhombifera. Jaekel (1900, p. 674) maintained Bather's Malocystidae only for *Malocystites* but placed it in the suborder Varicata (which is almost synonymous with Paracrinoidea), Order Eustelea (which bespeaks their simple columns) and Class Carpoidea. Jaekel (*op. cit.*), in a footnote stated that Bather's assignment of *Malocystites* to the Rhombifera was due to the close relationship of *Amygdalocystites*. He (Jaekel) further stated (in part erroneously) that *Amygdalocystites* has only radial ridges and no "fold-pores" as in cystoids.

Authors subsequent to Jaekel have maintained the same general grouping for *Malocystites* with other paracrinoid genera.

Regnéll (1945, p. 39) noted that "*Malocystites* is insufficiently known," *i.e.*, to be definitely included in the Class Paracrinoidea.

Kesling (1968, pp. 277-278) accepted *Malocystites* in this class, placing it in the Family Malocystitidae with *Wellerocystis*.

The morphology of the theca indicates a fairly close phylogenetic relationship with *Wellerocystis*; thus the assignment of these two genera to the family Malocystitidae.

Malocystites, its stratigraphic position notwithstanding, is morphologically the most specialized genus of the Paracrinoidea. Its ambulacra are the most extensively branched of the paracrinoids. The primary pinnule bases, so far as can be determined, are not particularly enlarged, which is a typical trait, and the arm lumens are apparently lacking. In addition, the recumbent pinnules are found only in this genus. The reduction and loss of these structures and simple sigmoidal arm suggests an advanced derivation from a simpler *Canadocystis*-like paracrinoid, which most probably had transverse exothecal or epithecal arms with large primary pinnule

bases and arm lumens. *Wellerocystis*, which is closely related, retains large arm lumens and large primary pinnule bases.

The theca, while not definitely known not to have a basic, fixed plate arrangement in juvenile forms, is made up of large, equidimensional plates, as compared to most paracrinoids that are constructed of relatively smaller and more irregularly shaped plates or more irregularly shaped plates. The greatly reduced hydropore is atypical and is regarded as a specialized feature, in view of its larger size in simpler genera. It is significant to note that simpler forms are more persistent and wide-spread in the geological record. Complex genera tend to be highly restricted stratigraphically and areally.

Sprinkle (1973, p. 185; 1973a, p. 870) speculated that *Malocystites* lived in turbulent waters in a manner (1973a) similar to the armless hybrocrinoid, *Tripatocrinus*. In his scheme, laminar flow passing over the theca at the end of a stiff column would produce a turbulent flow back-eddy on the lee side and would allow suspended food particles to be captured by the ambulacra. The authors concur with Sprinkle's interpretation in that the ambulacra in *Malocystites* is composed solely of recumbent pinnules, and this feature, along with the spherical shape of the theca, makes *Malocystites* well adapted to moderately strong currents.

The column, though virtually unknown, was, proximally at least, rigid, as evidenced by the short columnals with crenulate sutures, and probably was capable of holding the peristome uppermost in a current. As pointed out above, and by Sprinkle, 1973, the pinnule ossicles are deeply imbedded in the calluses, which gave extra strength. Lastly, *Malocystites*, like *Tripatocrinus*, is covered with coarse, pustulose prosopon. Currents flowing over such a surface would be broken up into small, turbulent back-eddies and probably would offset some of the current force directed against it.

***Malocystites murchisoni* E. Billings, 1858**

- 1858. *Malocystites murchisoni* Billings, E., Canadian Organic Remains, Dec. 3, Geol. Sur. Canada, pp. 66-67, pl. 7, figs. 1a-i.
- 1886. *Malocystis murchisoni* Billings, Haeckel, Die Amphorideen und Cystoideen, fest. Siebenzigsten Geburtsage von Carl Gegenbaur, Bd. 1, pp. 105-106.
- 1900. *Malocystites murchisoni* Billings, Jaekel, Deutsche Geol. Gesel., Zeit., Bd. 52, Hft. 4, pp. 674-675.

1968. *Malocystites murchisoni* Billings, Kesling, Treatise on Invertebrate Paleontology, Pt. S, p. 278.

Diagnosis, range, and description of this species is the same as that for *Malocystites* above. The genus, as now recognized (Jaekel, 1900, pp. 674-675) is monotypic.

Genus **WELLEROCYSTIS** Foerste, 1920

Type-species: *Wellerocystis kimmswickensis* Foerste, 1920.

Diagnosis.—Theca oval to subconical, composed of *c.* 40 generally irregularly hexagonal plates arranged in nine uneven, vertical-oblique rows. Three basals present. Two epithecal arms split laterally, resulting in four, five, or six dextrally spiraled branches; food grooves lateral, on concave curvature of each branch; arm lumens oval, extend length of arm; underarm thecal calluses prominent, grooved axially. Peristome at distal apex; posterior periproct closely adjacent. Column attachment offset antero-left laterally from bilateral plane of symmetry.

Range.—Middle Ordovician, Blackriverian, Kimmswick Limestone, Glen Park, Jefferson County, Missouri.

Description.—The theca is oval to subconical in profile and subcircular in cross section. It is composed of *c.* 40 plates, ranging from 36 to 44, most of which are irregularly hexagonal. Some four-, five- and seven-faceted plates are also present. Above the basals, the plates are arranged in nine vertical-oblique rows which distally are essentially parallel to the distal ends of the recumbent arms (Kesling, 1968, p. 278). Most rows are not more than four plates high above the basals. The lack of specimens, especially juveniles, precludes the determination of a basic number of plates and of a primary plate order. Intercalation of plates occurs primarily above the basals and may in some part be responsible for the oblique nature of the vertical rows. Intercalation probably continues throughout ontogeny, and in mature specimens occurs randomly on the upper half of the theca. The plates are essentially smooth with little evidence of pustulose prosopon.

There are three basals which are atypically to the anterior left, rather than the usual transverse-left. As in other platycystitids, there are two large, hexagonal, paired plates and a small, azygous, pentagonal plate making up this proximal circlet. The azygous plate

is anterior; the large paired plates are lateral and posterior. This contrasts with the Platycystitidae where the azygous basal is in the right-lateral position. Although the column is unknown, the attachment area indicates that it was circular in cross section. There is no evidence of a lumen at the common juncture of the basals.

In the three known specimens of *Wellerocystis* there is no evidence of either the hydropore or gonopore, and the specimens are oriented on the basis of the antero-left offset of basals and left offset of the peristome from the bilateral plane of symmetry. The periproct is immediately posterior to the peristome and the raised ambulacrum.

The peristome is apical, and at its transverse ends the arms split, each to form two or three branches (Pl. 13, figs. 4, 8, 9). This results in either four-, five- or six-armed types. Both Foerste (1920, p. 36) and Kesling (1968, p. 36) have reported that the holotype is a three-armed form, having a split left arm and a single right arm that partly encircles the periproct. Re-examination shows that the right arm also bifurcates, with the anterior branch almost obliterated in fossilization (Pl. 13, fig. 4).

Arm bifurcation or trifurcation occurs laterally to the transversely oriented oval peristome and the short transverse food grooves. On the left side, the proximal arm ossicle (the primary) is posterior to the transverse food groove. The first split in the main food groove occurs at the mid-length of the primary ossicle, with one branch, including the primary, extending onto the posterior face, the other onto the anterior. The main groove then traverses along the "primary" of the second arm, and at the distal end of this ossicle a bifurcation may occur, with a branch extending transversely along a short lateral arm. The right arm, to some degree, is a mirror image of the left. The primary ossicle is anterior to the transverse food groove. Usually the right arm is only bifurcated at the mid-length of the primary, with the branches extending onto the anterior (with primary ossicle) and posterior faces.

All of the arms spiral to the right (clockwise), and their external structure is typical for paracrinoids. Each main food groove faces essentially upward as in *Canadocystis*, not laterally as in *Amygdalocystites*, and each is located on the concave side of the branch. The

arms are relatively high in relief, as are the thecal calluses beneath them.

The thecal calluses are high and, like the arms, distally taper to plate level. Proximally, they achieve their maximum height at the bifurcation of the arms. Despite their marked prominence, they do not extend out beyond the width of the arms. In specimens where the arm ossicles are missing, a channel running the length of the callus is clearly visible. As in other paracrinoids, the arms have no allometric effect on the outlines of the plates.

The arm lumens extend the length of the arms. They are unusually large for paracrinoids (ca. 1.25 mm high proximally), oval in cross section, with the longer cross-sectional axis perpendicular-to-slightly-inclined to the surface of the theca. The lower one-third to one-fourth of the lumen is enclosed by the channel in the raised thecal callus (Pl. 13, figs. 5, 6, 8). The lumens appear to open (observation limited to one specimen) to the interior of the theca under the bifurcation or trifurcation area of each arm. No pinnular or external openings from the lumens have been observed, which seems to be the general case in the Paracrinoidea.

The left posterior arm of the holotype consists of 11 uniserial ossicles; the incomplete anterior branch may have had as many as 15. The posterior right branch has only four ossicles, but the abrupt termination of the arm and its callus suggests that the end may have been exothecal. In the other specimens, the ambulacra are poorly preserved or are incomplete. Apparently the left arms are composed of approximately the same number of ossicles as in the holotype. The posterior right arm branch has about 10 ossicles; the anterior right about six. No pinnules or covering plates are known.

Wellerocystis kimmswickensis Foerste, 1920 Pl. 13, figs. 1-13

1920. *Wellerocystis kimmswickensis* Foerste, Ohio Jur. Sci., vol. 21, No. 2, p. 37, text-fig. 1; pl. 1, figs. 12A, B.

1968. *Wellerocystis* [*kimmswickensis*] Foerste, Kesling, Treatise on Invertebrate Paleontology, Part S, p. 278, fig. 161.

Diagnosis, range, and description are the same as given in the generic analysis above.

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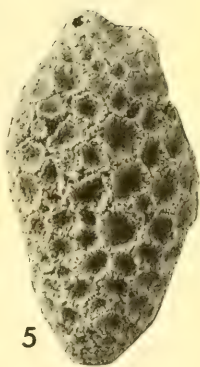
PLATES

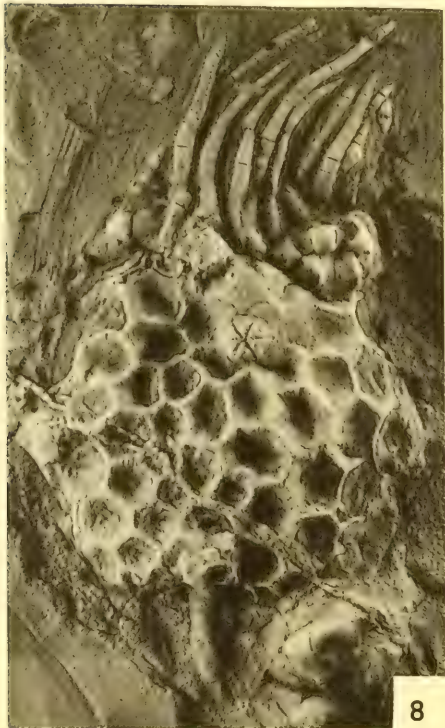
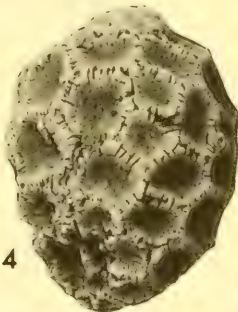
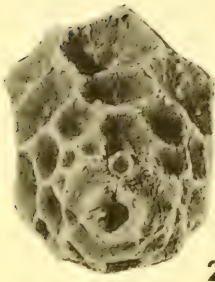
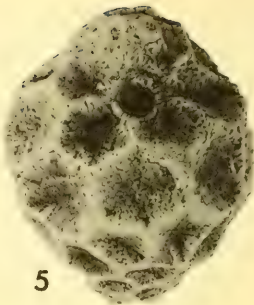
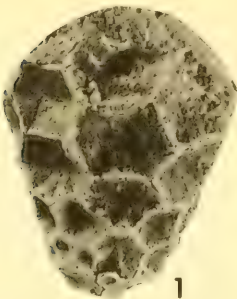
Explanation of the letter prefixes on the specimen numbers:

FMNH	Field Museum of Natural History
GSC	Geological Survey of Canada
ISM	Illinois State Museum
MCZ	Museum of Comparative Zoology, Harvard University
NYSM	New York State Museum
OU	University of Oklahoma
ROM	Royal Ontario Museum
SUI	State University of Iowa
UMMP	University of Michigan Museum of Paleontology
USNM	United States National Museum [National Museum of Natural History]
USNM(S)	United States National Museum, Springer Collection [National Museum of Natural History]

EXPLANATION OF PLATE 1

Figure		Page
1-3.	Comarocystites punctatus E. Billings	33
	1. An incomplete theca. Cobourg Fm., Ottawa, Ontario. Trentonian. Syntype. GSC 1391; $\times 1.5$. 2. Weathered theca with a part of one pinnulated arm preserved. ?Cobourg Fm., Ottawa, Ontario. Trentonian. Syntype. GSC 1391g; $\times 1.5$. 3. A nearly complete theca with a complete column and holdfast. Parts of two pinnulated arms are also intact. ?Cobourg Fm., Ottawa, Ontario. Trentonian. GSC 333a; $\times 0.75$.	
4-6.	Comarocystites tribrachius , n. sp.	34
	Dorsal, posterior and right lateral views, respectively, of the silicified theca. The three arm bases and the split in the covering plates over the sessile food groove are visible in figure 4. Curdsville Ls., three and one-half miles south of High Bridge, Ky. Trentonian. Holotype. USNM 93393. Fig. 4, $\times 2$; figs. 5, 6; $\times 1$.	



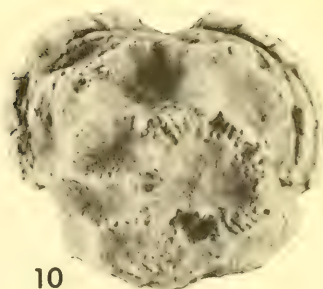
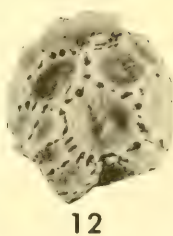
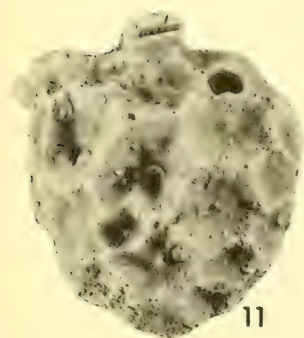
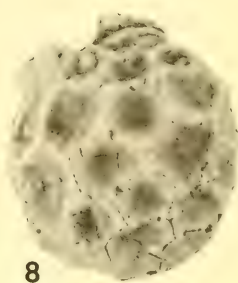
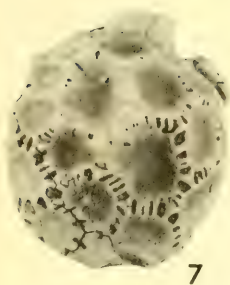


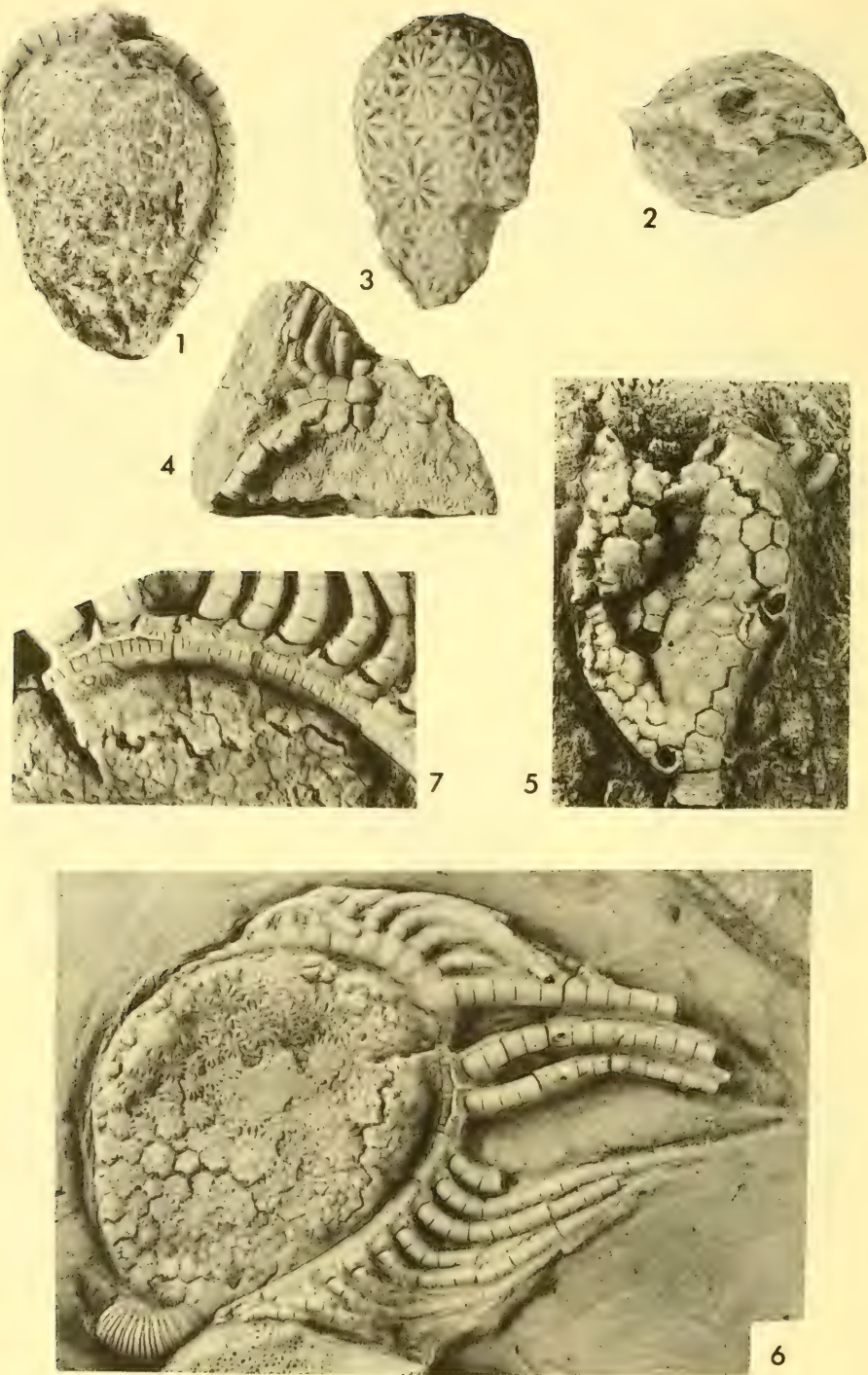
EXPLANATION OF PLATE 2

Figure		Page
1-7.	Comarocystites shumardi Meek and Worthen	36
	All specimens are from the Kimmswick Ls., Cape Girardeau, Mo., Trentonian. 1, 2. Lateral and transverse proximal views, respectively, of a " <i>C. obconicus</i> " type theca. Note small, inserted, concave platelets adjacent to the three basals. FMNH 10975; $\times 2$. 3. Part of a theca. FMNH 10975. Ca. $\times 2$. 4. Anterior or posterior face of a theca. Syntype of <i>C. shumardi</i> "var." <i>obconicus</i> . ISM 10473; $\times 2$. 5. Right lateral face with the periproct exposed. FMNH 10974; $\times 1.5$. 6. Proximal column and basal part of the theca. Syntype of <i>C. shumardi</i> "var." <i>obconicus</i> . ISM 10473; $\times 1.5$. 7. Theca with most of the distal part missing. Holotype. ISM 10472; $\times 1.5$.	
8.	Comarocystites punctatus E. Billings	33
	Right lateral face of a theca with pinnules bearing covering plates intact. The anal pyramid with six covering plates is also preserved. ?Cobourg Fm., Hull, Quebec. ROM 568T; $\times 1.5$.	
9.	Comarocystites shumardi Meek and Worthen	36
	Transverse food groove with bifurcations at each end leading to arm bases for exothecal arms. Kimmswick Ls., Interstate 55 near Barnhart, Mo. SUI 36522; $\times 2.5$.	

EXPLANATION OF PLATE 3

Figure		Page
1-10.	<i>Sinclairiocystis praedicta</i> Bassler	43
	All specimens, Mountain Lake Member, Bromide Fm., Black-riverian, from outcrops south of Sulphur, Okla., on U.S. 177 (distances measured from the junction of state highway 7).	
	1. Posterior face of the theca with eroded-exposed transutural slits. Anomalous pore present; 1.8 miles south of Sulphur, Okla. Holotype, USNM 116332; $\times$ 2. 2. Posterior face of a theca with slits exposed. Anomalous pore present; 1.8 miles south of Sulphur, Okla. USNM specimen; $\times$ 2. 3. Posterior face of a theca with transutural slits slightly exposed; 1.8 miles south of Sulphur, Okla. OU 7913; $\times$ 2.5. 4-6. Anterior dorsal and posterior faces of uneroded specimen. Note the pustulose prosopon uniformly developed on the theca and recumbent arms; 1.8 miles south of Sulphur, Okla. OU 7912; $\times$ 2. 7, 8. Anterior and posterior faces showing considerable variation in the eroded transutural slits. OU 8169; $\times$ 2. 9, 10. Dorsal and ?posterior faces of an enigmatic specimen. One of the arms is split, as evidenced by the single primary pinule. The food grooves are on the reverse sides of the arms and the "gonopore" is double. The "gonopores" may be gonopore and anomalous pore together. Using these pores as evidence to define the posterior face, the periproct is on the anterior face; 1.4 miles south of Sulphur, Okla. OU 7916; $\times$ 2.5.	
11.	Posterior face of a large theca slightly eroded; 1.4 miles south of Sulphur, Okla. OU 7914; $\times$ 2.	
12.	Anterior face of the small, slightly collapsed theca; 1.4 miles south of Sulphur, Okla. OU 7917; $\times$ 3.	



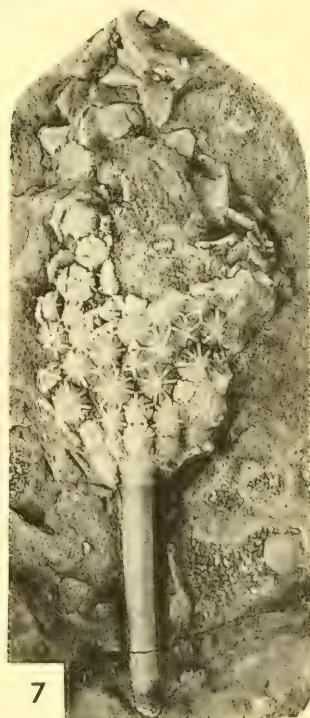
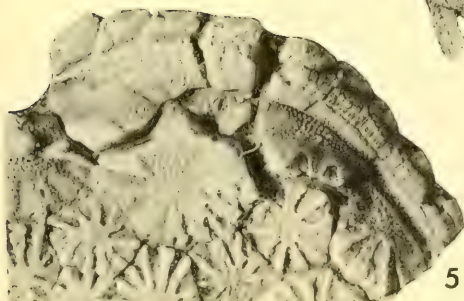
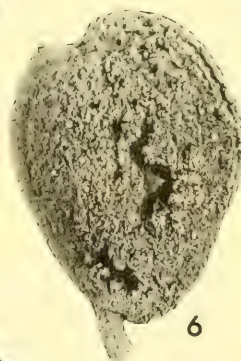
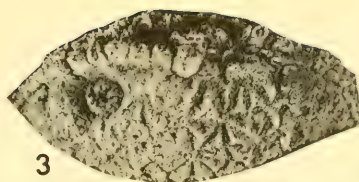
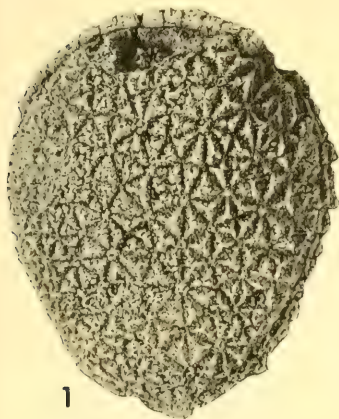


EXPLANATION OF PLATE 4

Figure		Page
1-7.	<i>Amygdalocystites florealis</i> E. Billings	49
	1, 2. Anterior and dorsal views, respectively of a theca. Cobourg Fm., Ottawa, Ontario. Trentonian. Holotype. GSC1396; $\times 1.5$. 3. Incomplete theca with an almost unweathered surface. Cobourg Fm., corner of Booth and Elm Streets, Ottawa, Ontario. GSC 9062; $\times 1$. 4. Distal part of a theca with parts of the recumbent arms and pinnules preserved. The extension of two pinnules from a single arm plate is atypical. Kirkfield Ls., Kirkfield, Ontario. Trentonian. USNM(S) 3104; $\times 2$. 5. Juvenile theca with parts of the recumbent arms and pinnules intact. Plates with only incipient development of sutural pores. Holotype of <i>Ottawacystites laevis</i> (W. R. Billings), Wilson = <i>A. florealis</i> herein. ?Hull Fm., Hull, Quebec. Trentonian. GSC 1395; $\times 3$. 6. Complete anterior face with most of the recumbent arms and pinnules intact. In this specimen the periproct is on the anterior face. Note the bend in the proximal column. ?Kirkfield Ls., Cambridge, Ontario. ?Trentonian. ROM 597T; $\times 2.5$. 7. Same specimen. Detail of the covering plates and pinnule bases of the left recumbent arm. $\times 3.8$.	

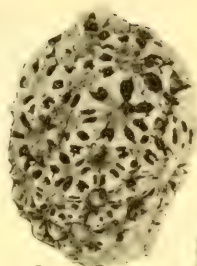
EXPLANATION OF PLATE 5

Figure		Page
1-6.	Amygdalocystites florealis E. Billings	49
	1-3. Anterior, posterior, and dorsal views of a silicified theca. Note the typical <i>A. florealis</i> prosopon. Holotype of <i>A. huntingtoni</i> Wetherby = <i>A. florealis</i> herein. Curdsville Ls., High Bridge, Ky. Trentonian. FMNH 6050; $\times$ 1.5. 4. Incomplete theca with parts of the recumbent arms and their covering plates intact. Kirkfield Ls., Kirkfield, Ontario. Trentonian. USNM(S) 3104; $\times$ 1.5. 5. Same specimen. Detail of the recumbent arm and its covering plates; $\times$ 4. 6. Posterior face of a silicified theca with part of the proximally bent column attached. Curdsville Ls., Curdsville, Ky. Trentonian. USNM 40965; $\times$ 1.5.	
7.	Amygdalocystites radiatus E. Billings	51
	Incomplete theca with part of the column attached. Note the distinct, narrow rays of the plate prosopon. Cobourg Fm., Ottawa, Ontario. Trentonian. Holotype. GSC 1394; $\times$ 1.5.	

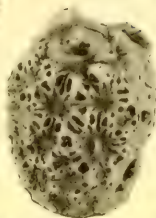




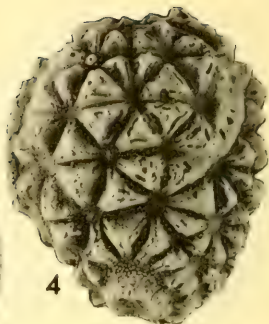
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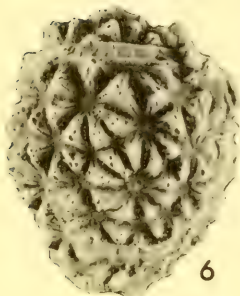
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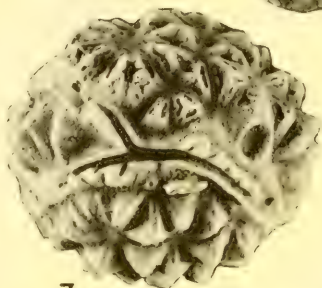
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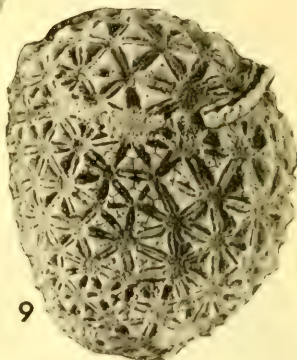
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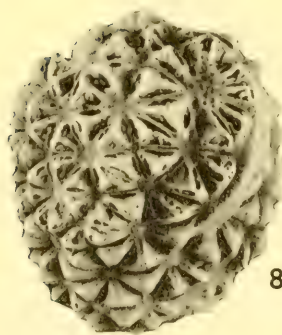
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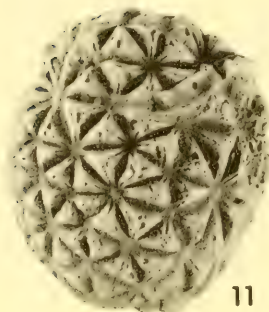
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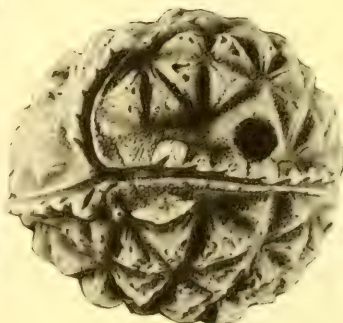
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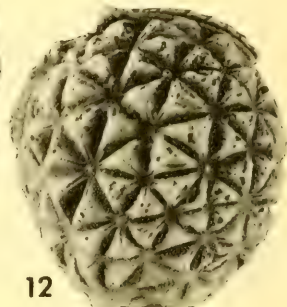
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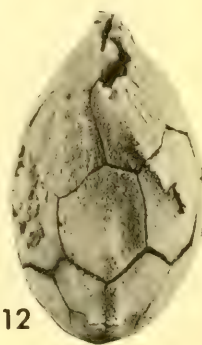
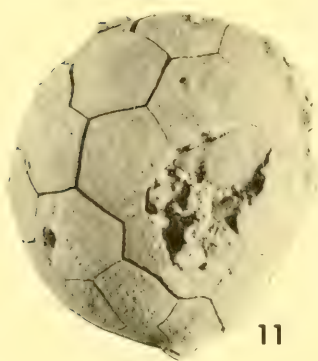
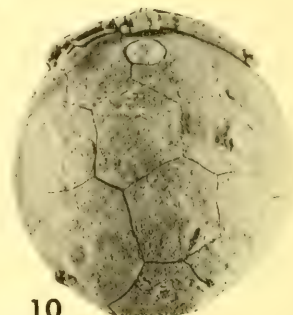
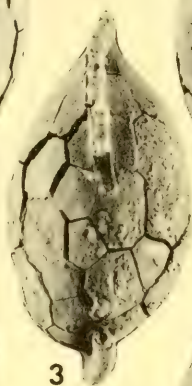
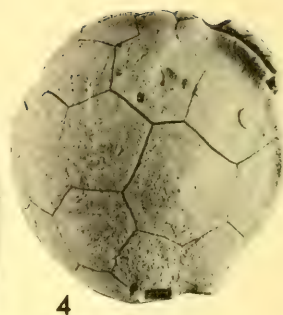
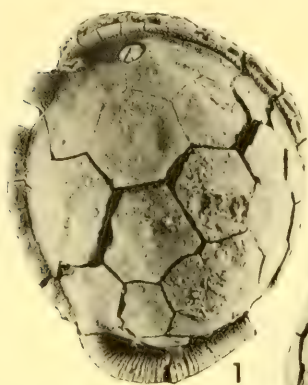
EXPLANATION OF PLATE 6

Figure		Page
1-13.	Oklahomacystis tribrachiatus (Bassler), n. genus	57
	All specimens from the Mountain Lake Member, Bromide Fm., Blackriverian; except for No. 1, all were found 100 feet west of road in NE $\frac{1}{4}$, SW $\frac{1}{4}$, SW $\frac{1}{4}$, sec. 3, T. 2S, R. 3E. (70 feet below Bromide-Viola contact) near Sulphur, Okla. 1. Posterior face of a poorly preserved and prepared theca. Holotype, <i>Amygdalocystites tribrachiatus</i> Bassler. Sec. 22, 2S, 3E, south side of the Arbuckle Mountains, Okla. USNM 93386; $\times$ 2. 2. Anterior face of an eroded juvenile theca. OU 7919; $\times$ 3. 3. Anterior face of a small, eroded juvenile theca. Note the numerous plates, indicating much of the thecal expansion is by peripheral plate growth. OU 7925; $\times$ 3. 4, 5. Posterior and dorsal faces of a mature theca. The transutural slit coverings or "epistereom" is only slightly eroded. The anomalous pore is directly proximal to the hydropore. OU 7023; $\times$ 2.25 and 2.5, respectively. 6. Anterior face of a slightly eroded theca. Both the anterior and left arms curve across this face. Note the prominent arm ossicle impressions. OU 8150; $\times$ 2. 7, 8. Dorsal and posterior faces of a mature, vari- ously eroded theca. The gonopore and hydropore are well developed. Note the double slit arrangement across the juxtaposed plate facets in fig. 8. OU 7924; $\times$ 2.5 and 2.25, respectively. 9. Anterior face of a large, eroded theca. Note the plate sutures on the weathered areas. OU 7926; $\times$ 2. 10. Anterior face of a small theca. Note the weathered, double transverse slits. OU 7921. $\times$ 2.5. 11, 12, 13. Anterior, posterior, and dorsal faces of a slightly eroded theca. The passageways under the surfaces of the trigonal pyramids are in some places unroofed, i.e., the "epistereom" is in some places removed. OU 7922; $\times$ 2.2 and 2.5, respectively.	

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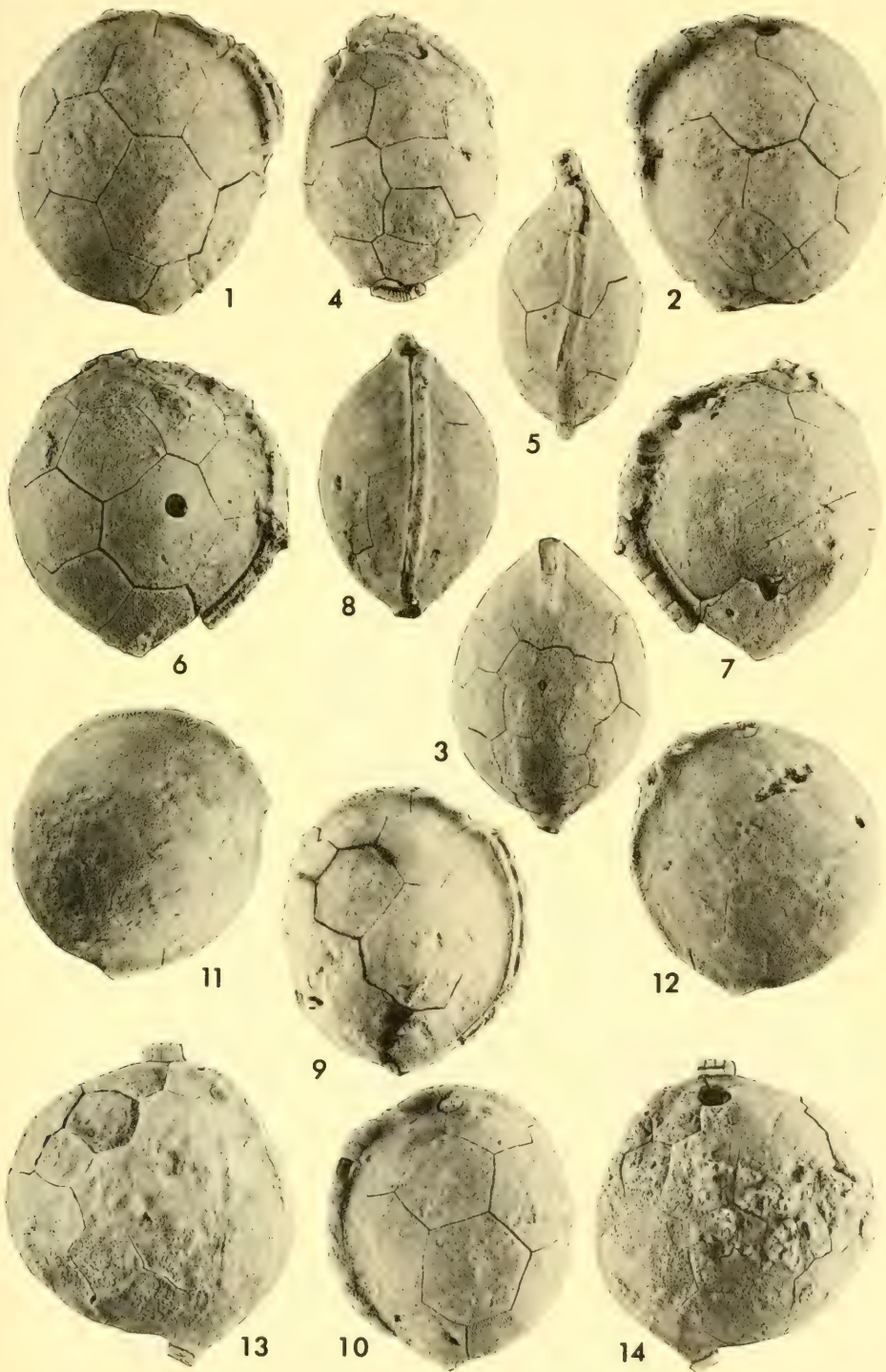


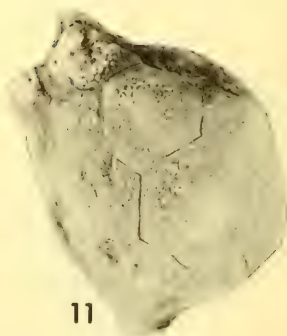
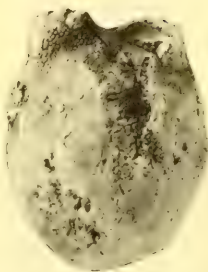
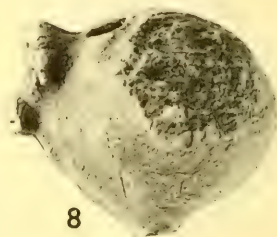
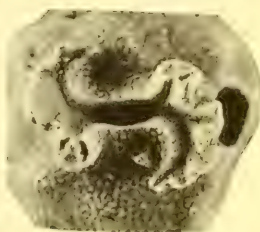
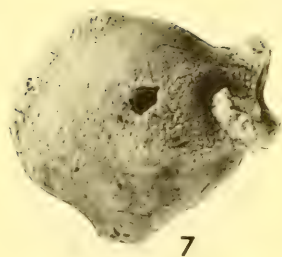
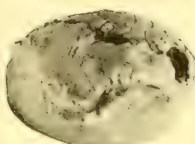
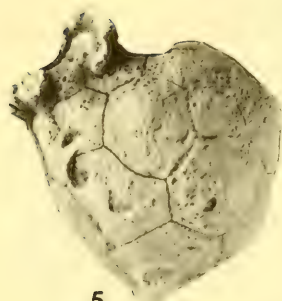
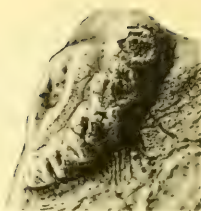
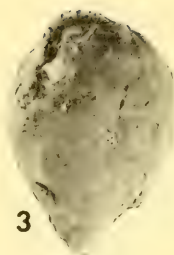
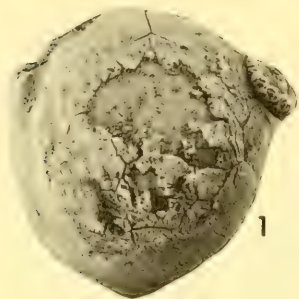
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	All specimens from Daube Ranch, west of the west branch of Sycamore Creek, SW $\frac{1}{4}$, SE $\frac{1}{4}$, NW $\frac{1}{4}$ of Sec. 27, T3S, R4E, Johnson Co., Okla. (238 feet below the contact with the Viola Ls.). Mountain Lake Member, Bromide Fm. Black-riverian. 1-3. Posterior, left and right faces of a large theca with arms, anal pyramid, and the proximal column attached. Many intercalates, and many plates are hard to identify. OU 8158; $\times 1.5$. 4-6. Anterior, right, and left faces of a well-preserved theca. Note the numerous intercalates on the right face and the well-defined arm callus on the left. OU 8164; $\times 1.5$. 7, 8. Anterior and posterior faces of a mature theca with a somewhat elongated profile. OU 8168; $\times 1.25$. 9, 10. Anterior and posterior faces of a mature, rounded theca with some of the right arm intact. The anal pyramid is well preserved. OU 8161; $\times 1.25$. 11-13. Anterior left and posterior faces of a mature theca. The left arm curves onto the posterior face. Note the ridge on plate Ll 1 (just dorsal to the vertical suture of the basals) which is normally under the arm. OU 8162; $\times 1.5$.	

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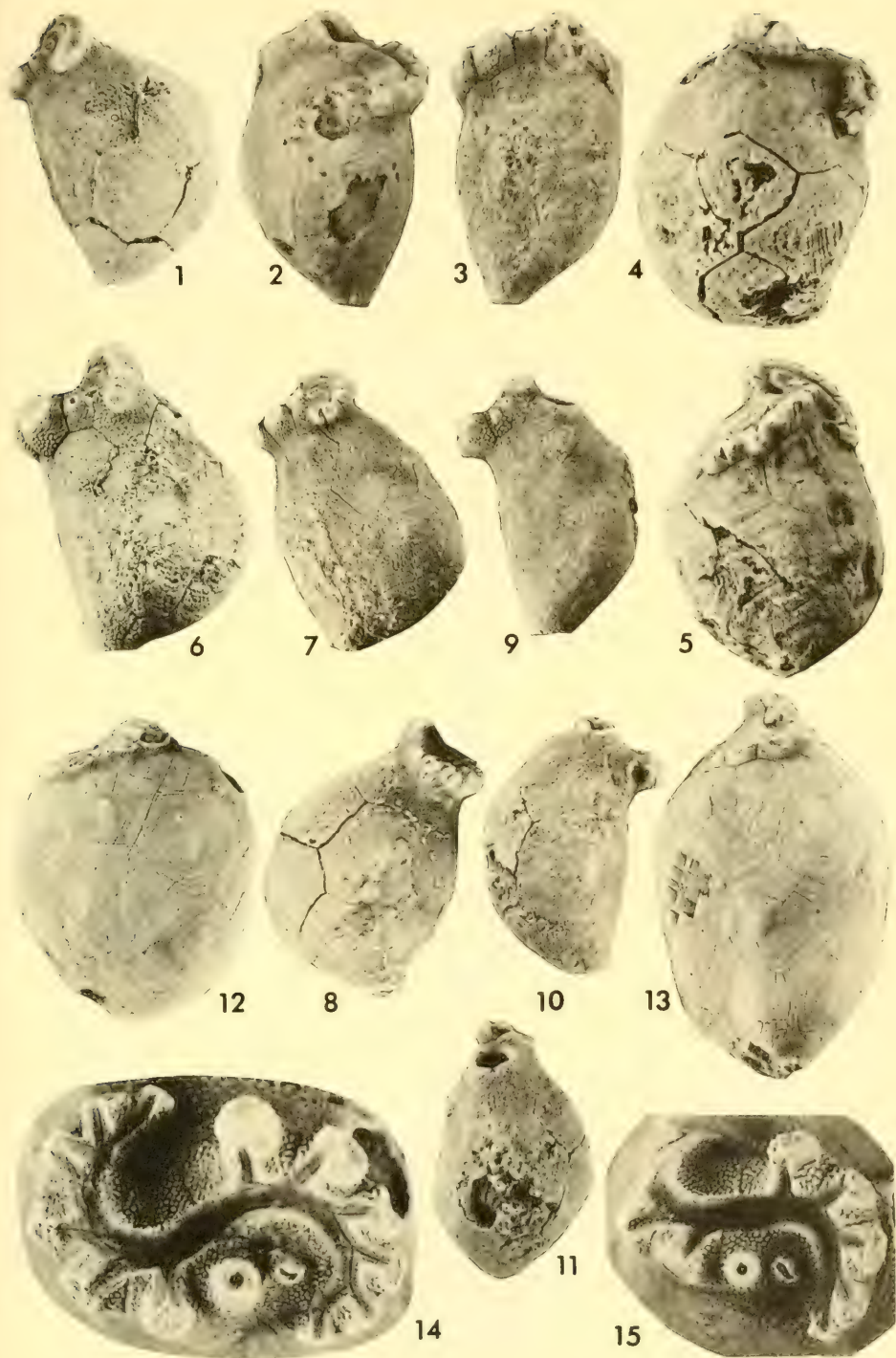
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	All specimens from the Island of Montreal, Quebec. (?) Laval Ls. Chazyan. Syntypes. 1, 2. Anterior face and detail of the left arm. Note the deep ligamental pits on the upper arm surface. GSC 1011b; $\times 1.5$ and $\times 5$, respectively. 3, 4. Posterior and dorsal face of an elongate, badly eroded theca. GSC 1011a; $\times 2$. 12. Anterior face of a small, worn theca. Note the pustulose prosopon under the recumbent arm. GSC 1011c; $\times 3$.	
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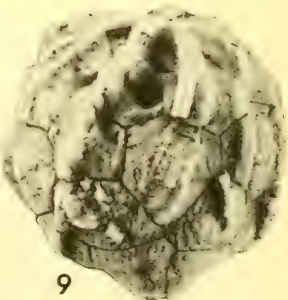
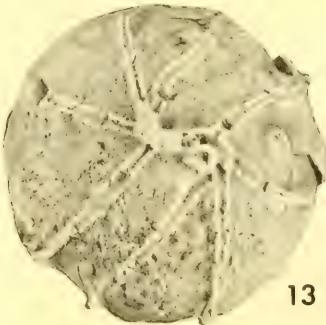
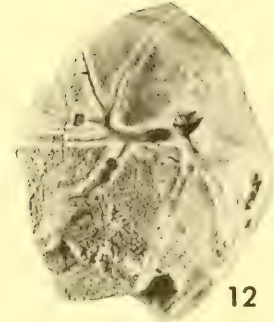
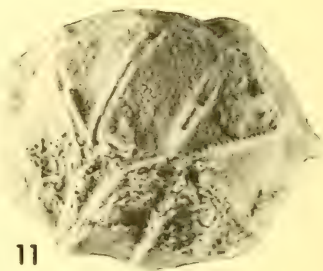
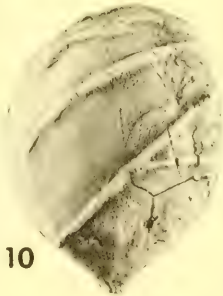
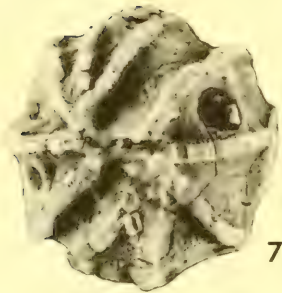
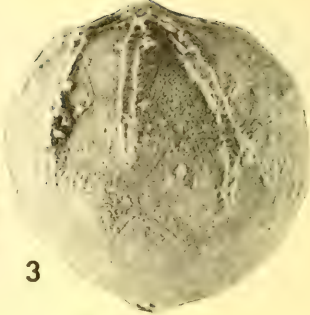
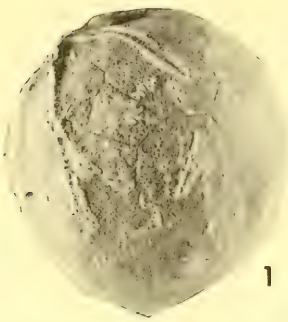
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Figure

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- 1-15. **Canadocystis tennesseensis**, new sp. 76
1. Posterior face of a theca. Wardell Ls., Evans Ferry, Tenn. Blackriverian. Holotype. USNM 93378; $\times$ 3.0. 2, 3. Anterior and posterior faces of a small, somewhat eroded theca. Wardell Ls., Evans Ferry, Tenn. Blackriverian. Paratype. USNM 93355; $\times$ 5. 4, 5. Anterior and left faces of a mature, eroded theca. Wardell Ls., Evans Ferry, Tenn. Blackriverian. Paratype. USNM 93378a; $\times$ 3.5. 6. Posterior face of a theca. Pustulose prosopon on the oral end of the theca is well preserved. Benbolt Fm., Red Hill, Tenn. Blackriverian. Paratype. USNM 93377; $\times$ 4.5. 7, 8. Posterior and anterior faces of a theca. Benbolt Fm., Red Hill, Tenn. Blackriverian. Paratype. USNM 93359; $\times$ 3. 9-11. Posterior, anterior, and right faces of a small theca. Wardell Ls., Evans Ferry, Tenn. Blackriverian. Paratype. USNM 93355a; $\times$ 5. 12. Posterior face of a large, eroded theca. Lenoir Ls., $\frac{1}{4}$ mile west of Friendship, Tenn. Chazy(?) Paratype. USNM 93371a; $\times$ 2. 13. Left face of a large, eroded theca. Some growth banding is visible, as it is in No. 12. Lenoir Ls., $\frac{1}{4}$ mile west of Friendship, Tenn. Chazy(?) Paratype. USNM 93371; $\times$ 2. 14. Dorsal (oral) view of the sigmoidally arranged recumbent arms. Note that the sutures between the arm ossicles and the underlying thecal plates are on the bottom of the main food groove. The gonopore and hydropore are well developed. Lincolnshire Fm., Luttrell, Tenn. Blackriverian. Paratype. USNM 93376; $\times$ 6. 15. Dorsal view of a nearly complete ambulacrum. Lincolnshire Fm., Luttrell, Tenn. Blackriverian. USNM 93376a; $\times$ 7.



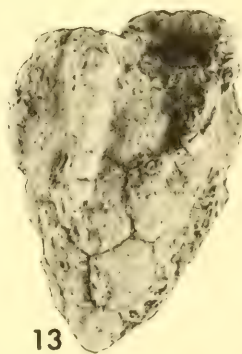
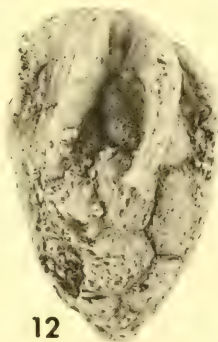
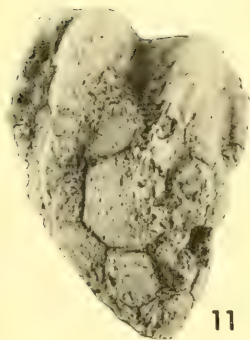
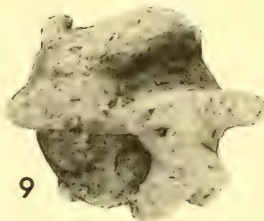
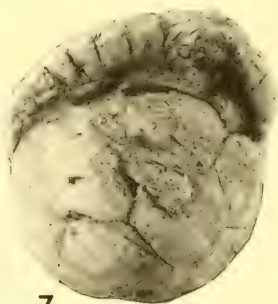
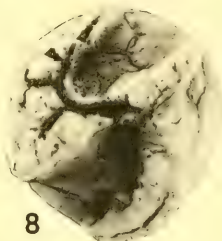
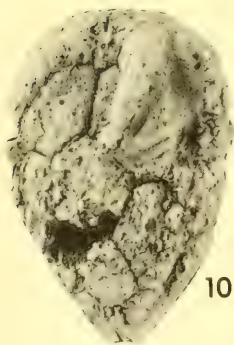
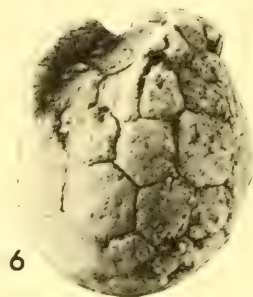
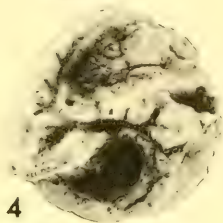
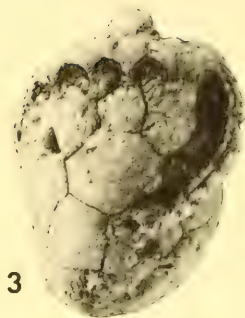
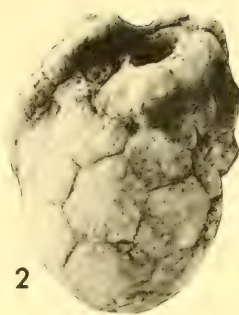
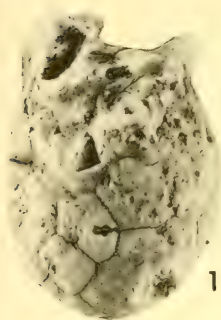


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1-13.	Malocystites murchisoni E. Billings	91
	All specimens from the Chazy Ls., Chazyan. 1-3, 5. Right, dorsal, posterior, and ventral faces of a theca. Pinnule scars are visible radiating from the peristome. Isle of Montreal, Quebec. Syntype. GSC 1012d; $\times$ 2.5. 6. Left face (?) of a theca with a short length of the proximal column attached. Isle of Montreal, Quebec. Syntype. GSC 1012; $\times$ 2.25. 7-9. Dorsal, left, and posterior faces of a small theca. Note on the dorsal view that there are five recumbent pinnules. Isle of Montreal, Quebec. UMMP 60847; $\times$ 3.5. 11. Dorsal face of a theca with several complete recumbent pinnules. Alymer Fm., C.P.R.R. tracks at Blvd. Cartier, Ville de Laval, Quebec. MCZ 718a; $\times$ 2.25. 12. Dorsal face of a theca with pinnule scars. Alymer Fm., C.P.R.R. tracks at Blvd. Cartier, Ville de Laval, Quebec. MCZ 718c; $\times$ 2.25. 13. Dorsal face of a theca with pinnule scars and anal pyramid. Alymer Fm., C.P.R.R. tracks at Blvd. Cartier, Ville de Laval, Quebec. MCZ 718b; $\times$ 2.	

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By

W. A. VAN DEN BOLD

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OSTRACODES FROM THE LATE NEOGENE OF CUBA

W. A. VAN DEN BOLD
Louisiana State University

ABSTRACT

Distribution of ostracodes in the late Neogene of the region around the towns of Matanzas and Santiago de Cuba is tabulated and the majority of the species is described and figured or figured. In both areas deposition took place in shallow marine environment with horizons of reduced salinity and the sediments range from fairly coarse clastics to reefal limestones. In the Matanzas region the age of the deposits varies from early Pliocene to late Pliocene or early Pleistocene; in the Santiago region the La Cruz Formation is of late Pliocene age. Three new species (*Procythercis? howei*, *Perissocytheridea pumila*, and *Perissocytheridea compressa*) are described from the La Cruz Formation.

INTRODUCTION

In 1964 Sandberg redescribed the species *Cyprideis subquadraregularis* (Brady) from Brady's original material of the harbour of Santiago de Cuba. At the time he expressed the opinion that this species was derived, and I suggested to him, that the only known beds where it could have come from were those of the La Cruz Formation, outcropping in and around Santiago. In 1946 I had described a few samples from the La Cruz Formation in which I did not recognize this large *Cyprideis* species and the fauna of which did not suggest at that time a different age than that of middle Miocene, which it had been given by Vaughan as early as 1919.

In 1972 I visited Santiago with the aim of finding out where *Cyprideis subquadraregularis* really came from, and I found it even before making the visit when I examined a slide from a waterwell, drilled at the School of Medicine of the University of Oriente, in the collections of the Dirección General de Geología y Geofísica in Habana, which well was reported to have been drilled in the La Cruz marl. Also this slide showed the presence of other species which suggested a much younger age than the one hitherto assumed. As a matter of fact, it is similar to that of the Canímar Formation of Matanzas, which I had collected previously. Therefore, there was here an opportunity to compare the La Cruz Formation with the Canímar Formation, some samples of which can be dated accurately by means of planktonic Foraminifera. However, here another problem occurs, namely that of rapid facies changes within the Canímar Formation and associated other formations, a problem that has been dealt with by several Cuban paleontologists, but which could stand some further examination based on other parts of the abundant fauna, in this case on the ostracodes.



Text-figure 1.—Map of Cuba, showing the location of Matanzas (Text-fig. 2), Santiago de Cuba (Text-fig. 4), and places along the north coast, from which ostracodes are listed in Table 5.

RECENT FAUNA

From the “Rade de Santiago” Brady (1870, pp. 237-239) described the following species:

Bairdia dextvattrei, *Bairdia victrix*, *Cythere compacta*, *Cythere pumicosa*, *Cythere subrugosa*, *Cythere perieri*, *Cytheridea similis*, *Cytheridea subquadraregularis*, *Loxoconcha levis*, *Loxoconcha elegans*, *Xestoleberis margaritea*, *Cytherella polita*. In a sample from the same general areas in the H. V. Howe collections I found: *Cytherella polita* Brady, *Cytherella semitalis* Brady?, *Cyprideis similis* (Brady), *Perissocytherides subrugosa* (Brady), *Cativella navis* Coryell and Fields, *Orionina serrulata* (Brady), *Cytheretta pumicosa* (Brady), *Radimella* sp. 2, *Loxoconcha levis* Brady, *Cytherura* sp. aff. *C. johnsoni* Mincher, *Paracytheridea* sp., *Pellucistoma* sp., “*Leptocythere*” *yoni* Puri, *Paracytheroma* sp., *Xestoleberis* spp.

From a comparison of the two lists differences in the faunas are striking and it is clear that the samples did not come from the same locality: absence of *Bairdia*, *Campylocythere?* *perieri* (Brady), and *Cyprideis subquadraregularis* (Brady) in our sample, absence of e.g. *Orionina serrulata* and *Cytherella semitalis?* in Brady's sample. The possibility exists that *Radimella* sp. 2 was referred to by Brady as *Cythere compacta*, in which case it was certainly different from the original species described by Brady. J. W. Teeter is

describing this form from British Honduras for which reason it is not named here. For comparison with the fauna of the Cuban North Coast, especially the Habana-Matanzas area, see Table 5.

YOUNG NEOGENE OF MATANZAS

HISTORICAL REVIEW

It is not intended here to give a complete review of the confusion concerning the use of the names Matanzas, Canímar, El Abra, and Capas de *Gypsina*. This was done by de la Torre (1966), Iturralde Vincent (1969), and Bermúdez (1967), see Table 1.

1) Canímar Formation and Capas de *Gypsina*.

Brödermann (1940, p. 20; 1942, p. 17) established the name Capas de *Gypsina* for beds in this region with abundant *Gypsina pilaris* (Brady); later (1945, pp. 132, 145), he proposed for these beds the name Canímar Formation with type locality 800 m from the mouth of the Rio Canímar (loc. 1583 of Palmer, 1948 — loc. 218 of Bermúdez in Palmer and Bermúdez, 1936). Beds at this locality do not contain (abundant) *Gypsina pilaris*.

Bermúdez (1950, pp. 302-305) proposed the name Canímar Formation for beds outcropping about 3 km south of the mouth of this river (Bermúdez loc. 222) which do contain *Gypsina pilaris*. This locality lies at least 70-80 m below Brödermann's type locality. This discrepancy was discussed by de la Torre (1966), who accepts Canímar and Capas de *Gypsina* as different facies of the same stratigraphic unit. As a result of de la Torre's work Bermúdez (1967) restudied the planktonic Foraminifera of the two samples. Adjusted to the latest views on planktonic zonation (Lamb and Beard, 1972) loc. 218 has to be placed in the upper Pliocene, loc. 222 in the lower Pliocene. Bermúdez (1967) suggested that loc. 222 (upper Miocene according to his scale) represents the top of the Cojímar Formation. Iturralde Vincent (1969) accepting Bermúdez' age determinations placed the Capas de *Gypsina* in the upper Miocene, the Canímar in the upper Pliocene, separated by an hiatus.

Spencer 1894	Brodermann 1945	Bermúdez 1950	de la Torre 1966	Bermúdez 1967	Iturralde 1969	Present Report
Matanzas			Matanzas	Matanzas		Matanzas = ? Canimar
		Pleistocene		El Abra mar	El Abra mar	El Abra
Miocene	Canimar C. de Gypsina	Pliocene		El Abra mar	C. de Gypsina	C. de Gypsina
		Miocene	El Abra mar	El Abra mar	El Abra mar	El Abra
Eocene	Guines	Miocene	El Abra mar	El Abra mar	El Abra mar	Guines
		Eocene	El Abra mar	El Abra mar	El Abra mar	Guines

Table 1. Views on the stratigraphy of the Neogene of the Matanzas area from 1894 to the present.

2) El Abra Formation.

Bermúdez (1950, pp. 300-301) described the El Abra Formation from the gorge of the Río Yumurí near Matanzas City. This formation is considered by de la Torre (1966, p. 26) as an estuarine or mangrove facies of the Canímar Formation. Iturralde Vinent (1969, p. 17), on the other hand, separated it from the Canímar Formation proper and considered it as time equivalent of the Capas de *Gypsina*.

3) Matanzas Formation

Spencer (1894) established the Matanzas Formation with type locality below the Iglesia de San Pedro, Matanzas (loc. 7111 on text-fig. 2). Bermúdez (1950, pp. 302-305) used the name Matanzas Formation for the beds at his loc. 218, which as pointed out by de la Torre (1966) corresponds to the type locality of Brödermann's Canímar Formation. According to de la Torre the Matanzas Formation is probably Pleistocene in age, but older than the Jaimanitas Formation of Habana Province.

PRESENT STUDY (Text-figs. 2, 3)

In 1971 and 1972 I resampled the different localities of the Matanzas Neogene with the kind help of the Academia de Ciencias (Instituto de Geología) and the Dirección General de Geología y Geofísica. On these trips I was accompanied by Lenia Montero, Pavla Lubimova, Jorge Sánchez Arango, Alfredo de la Torre, and Primitivo Borro. See also the description of the localities.

1) Matanzas Formation (Spencer, 1894), loc. 7111.

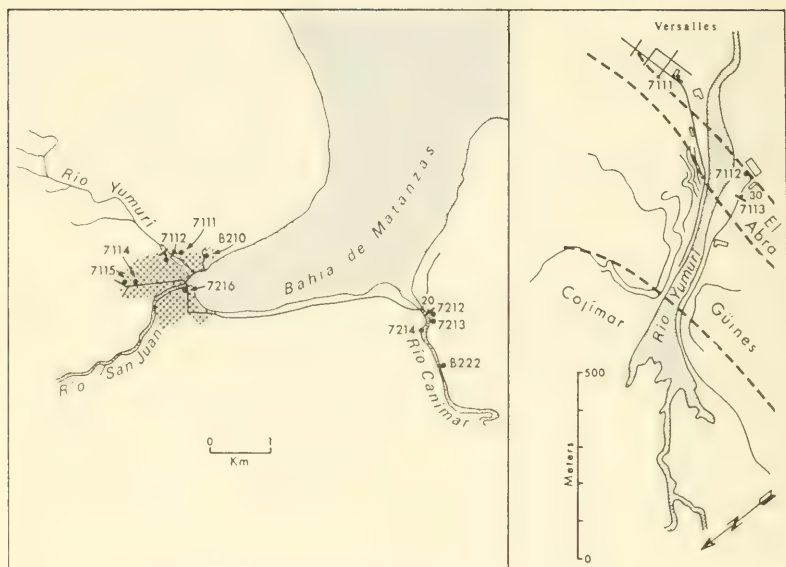
2) Canímar Formation (Brödermann, 1945): loc. 7212 — loc. 218 of Bermúdez.

3) Capas de *Gypsina* (Brödermann, 1945).

These beds crop out in several places within the limits of the City of Matanzas and as type locality the outcrops near the Hospital de Homicultura have been considered (Carretera Central around km 100): loc. 7114, 1715.

4) El Abra Formation (Bermúdez, 1950), loc. 7112.

In addition several other localities were sampled, one of which (7216) yielded a rich ostracode fauna. Prior to this I had received material from P. Bermúdez from his localities 210, 218, and 222.

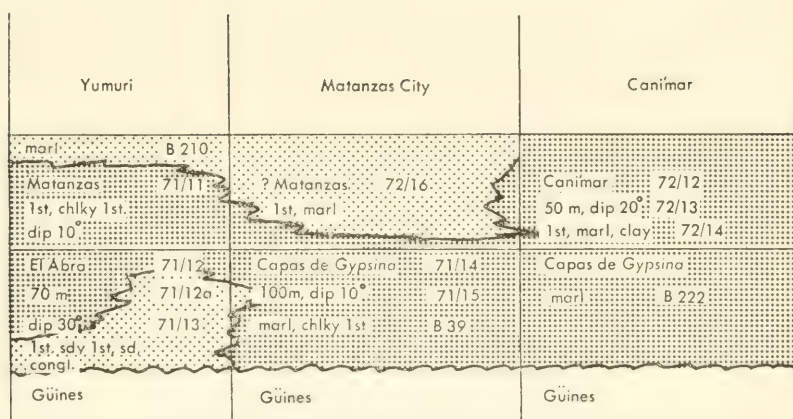


Text-figure 2. Location of samples in the Matanzas area.

The position of Bermúdez 210 is not certain in relation to loc. 7111 (Matanzas Formation), it may lie just above or below this level. I also received from Iturralde Vinent material from localities MI-43 and 44 at the Hospital de Homicultura, which corresponds to my localities 7114 and 7115.

Near the Hospital de Homicultura the Capas de *Gypsina* directly overlies the Güines Formation. In the Yumurí Valley the El Abra Formation overlies the Güines Formation which in turn overlies the Cojímar Formation. The nature of the contact between El Abra and Güines and Capas de *Gypsina* and Güines is not clear. A comparison between the three sections (Yumurí River, Matanzas City and Canímar River) is given in Text-figure 3.

The age of the Canímar Formation at its type locality is late Pliocene on the basis of planktonic Foraminifera (Bermúdez, 1967) whereas the age of the Capas de *Gypsina* is early Pliocene. The overall Pliocene age of the whole section along the Canímar River is con-



Text-figure 3. Schematic diagram of the stratigraphic relationship of localities in the late Neogene of Matanzas. Widely dotted: brackish-water facies; densely dotted; marine facies.

firmed by the presence of *Radimella confragosa* (Edwards) throughout. A late Pliocene of younger age is suggested for the Matanzas Formation and localities 6216 and B 210 (? Matanzas Formation) and the Jaimanitas Formation by the presence of ostracodes which in various places have been found in latest Pliocene or Pleistocene sediments: *Cyprideis bensoni* Sandberg, *Radimella* sp. 2 (Caloosahatchee, Manchioneal), *Loxoconcha levis* Brady (Mao), *Loxoconcha ochlockoniensis* Puri and *Uroleberis angulata*. *Hemicyprideis? setipunctata* (Brady) appears to occur only in the younger part of this section. If the author's feeling that *Radimella* sp. 2 does not appear earlier than the base of the Pleistocene is correct, then the Jaimanitas, Matanzas, and ? Matanzas Formations (B 210) belong to this period. However, the Matanzas Formation might be late Pliocene in age and equivalent to the Canimar Formation, in which case the separation of the two formations might be questioned.

[illegible]

Table 3: Species counts of samples or groups of samples in the Matanzas upper Neogene, indicating number of species in common between groups.

	Jaiman- itas	Matan- zas	B210	72/16	Canímar	B222	C. de <i>Gypsina</i>	El Abra
Jaimanitas	16	4	11	7	9	6	7	2
Matanzas	4	10	8	5	7	4	7	2
?Matanzas (B210)	11	8	34	11	12	6	7	3
?Matanzas (7216)	7	5	11	14	11	7	10	4
Canímar	9	7	12	11	32	14	19	5
C. de <i>Gypsina</i> (B222)	6	4	6	7	14	15	10	3
C. de <i>Gypsina</i> (type)	7	7	7	10	19	10	24	4
El Abra	2	2	3	4	5	3	4	6

In Table 3 counts of species present in samples or groups of samples are given of the Matanzas, Jaimanitas, Canímar, El Abra Formations, and Capas de *Gypsina*, and locations questionably correlated with the Matanzas Formation (B 210, 7216). This shows:

- 1: Canímar type (32 species) has 19 species in common with the Capas de *Gypsina* type (24 species) and 14 with the immediately underlying Capas de *Gypsina* (15 species).
- 2: The two questionable Matanzas Formations have 11 species in common. Sample B 210 contains 8 of the 10 species of the type Matanzas.
- 3: The El Abra Formation has only six species: it shows least correlation with the Matanzas Formation and Jaimanitas Formation, most with the Canímar and Capas de *Gypsina*.

LOCALITIES AROUND MATANZAS (Text-fig. 2)

- 7111: Pocket of soft marl in massive coral limestone. Cut in calle de la Nueva Esperanza, below Iglesia de San Pedro, Versalles, Ciudad de Matanzas. Type locality of Matanzas Formation, Spencer 1894.
- 7111, 12a: Soft sandlens in hard coral limestone, dipping about 30°S. Tannery "Progreso" Comp. Cortidora Cubana.
- 7113: Sandlens about 24 m below 7112, about 20 m above the base of the El Abra Formation: Type locality of El Abra Formation, Bermúdez, 1950.
- 7114: Light cream-colored, loose marl with *Gypsina pilaris*, at the entrance to the Hospital de Homicultura, opposite Parque Rene Fraga, Matanzas.
- 7115: Sandy, cream-colored marl with *Gypsina pilaris*, immediately above Güines Limestone. Cut in Carretera Central at km 100.

- 7212: Nodular, cream-colored marl with beds of fingercorals, between thick banks of limestone, 200 m upstream from the Highway bridge, at the Manatíal de agua, just to the right of the pumping station. B. 218. Type locality of the Canímar Formation, Brödermann, 1945.
- 7214: Grayish, sandy clay with gypsum on W bank of the Río Canímar.
- 7216: S bank of the Río San Juan, below Sánchez Figueras bridge: soft weathered marl between banks of coral limestone.
- Berm. 210: Weathered arenaceous marl, cut at calles Santa Rita and San Juan de Diós, Matanzas.
- Berm. 222: Soft cream marl, Río Canímar, 2 km south of Antiguo Andaribal. Type locality of Canímar Formation of Bermúdez, not Brödermann.

YOUNG NEOGENE OF ORIENTE

LA CRUZ FORMATION (Vaughan, 1919)

Type locality. — Loma La Cruz, Santiago de Cuba.

Lithology. — Soft limestone with abundant macrofauna, with at the base intercalations of conglomerate and sand.

Historical review. — Vaughan (1919, pp. 218, 595) used the name La Cruz marl, which was given formational status by Lewis and Straczek (1955, pp. 187, 272, 275). The most complete faunal information is given by Keijzer (1943, pp. 106-107, table 16), who reported on the foraminiferal fauna of samples collected by H. J. Tschopp. The ostracodes from these samples were listed by van den Bold (1946).

No data have been presented that allow a precise age assignment of the formation: Cooke (1919) on the basis of mollusks, compared the La Cruz marl with the Anguilla Limestone of Anguilla, and the Tampa Limestone of Florida, both now considered lower Miocene. Vaughan (1919) on the basis of the corals, claimed these beds to be younger than the Bowden Formation, at that time accepted at middle Miocene but now considered to be Pliocene (Robinson, 1969, van den Bold, 1971, Lamb and Beard, 1972). Bermúdez (1949, pp. 298-300) placed the La Cruz Formation at the same level as the Canímar Formation (middle Miocene, acc. to Bermúdez, 1949, pp. 295-298), but of different facies, namely shallow marine, similar to the facies of the Güines Formation. De la Torre (1966) supported this correlation but did not present additional data.

PRESENT STUDY

The following species of ostracodes were originally determined in the La Cruz Formation (van den Bold, 1946). Present names have been added.

- Cytherella burcki* van den Bold = *Cytherella polita* Brady
Cytherella cubensis van den Bold = *Cytherella* sp.
Erythrocypris dreikanter (Coryell and Fields) = *Propontocypris* sp.
Pontocypris dactylus (Egger) = *Paracypris* sp.
Paracypris polita Sars = *Paracypris choctawhatcheensis* Puri
Bythocypris pachyconcha van den Bold = *Disopontocypris pachyconcha* (van den Bold)
Bairdia antilla van den Bold = *Bairdia antillea* van den Bold
Bairdia amygdaloides Brady = *Bairdia "amygdaloides"* Brady
Bairdia amygdaloids var. *oblonga* van den Bold = *Bairdia oblonga* van den Bold
Cytheridea (*Haplocytheridea*) *stephensoni* van den Bold = ? *Cyprideis bensoni* Sandberg ♀
Cytheridea (*Haplocytheridea*) *cubensis* van den Bold = ? *Cyprideis bensoni* Sandberg ♂
Perissocytheridea matsoni (Stephenson) = *Perissocytheridea* sp.
Cythereis vaughani (Ulrich and Bassler) = *Orionina serrulata* (Brady)
Hemicythere antillea van den Bold = *Quadracythere compacta* (Brady)?
Brachythere deformis (Reuss) = *Procythereis?* howei, n. sp.
Loxococoncha antillea van den Bold + var. *nodosa* = *Loxococoncha fischeri* (Brady)
Xestoleberis sp. A. = *Xestoleberis* sp. 1

The majority of the ostracodes of the La Cruz Formation also occur in the shallow water upper part of the Lower Coastal Group of Jamaica (van den Bold, 1971). In addition the following brackish-water species occur:

- Cyprideis subquadraregularis* (Brady), reported originally from Recent sediments in Santiago Bay (reworked) and subsequently found in the "Lajas" beds of Puerto Rico and the Las Salinas Formation of the Dominican Republic.
Cyprideis salebrosa van den Bold, originally described from the upper Pliocene Talparo Formation of Trinidad and later found in many localities of the Caribbean and Gulf of Mexico: Upper Las Salinas Formation and Jimaní Formation (Dominican Republic), uppermost Las Cahobas Formation (Haiti), uppermost "Lajas" beds (Puerto Rico).
Cyprideis bensoni Sandberg, originally described from Recent sediments of the Gulf of Mexico, found in the young Neogene of Costa Rica and the uppermost Las Cahobas Formation of Haiti.

Based on the presence of *Radimella confragosa* (Edwards) the age of the La Cruz Formation is Pliocene or younger and the combination of the three brackish-water species mentioned above indicates that at least part of it is late Pliocene. Comparison of the

Table 4. Distribution of ostracodes in the La Cruz Formation, Santiago de Cuba, separated into two sections, one north and one south of the town. No stratigraphic superposition of the sections implied.

fauna of the Ponce and "Lajas" beds of Puerto Rico indicates that these beds are of nearly equal age.

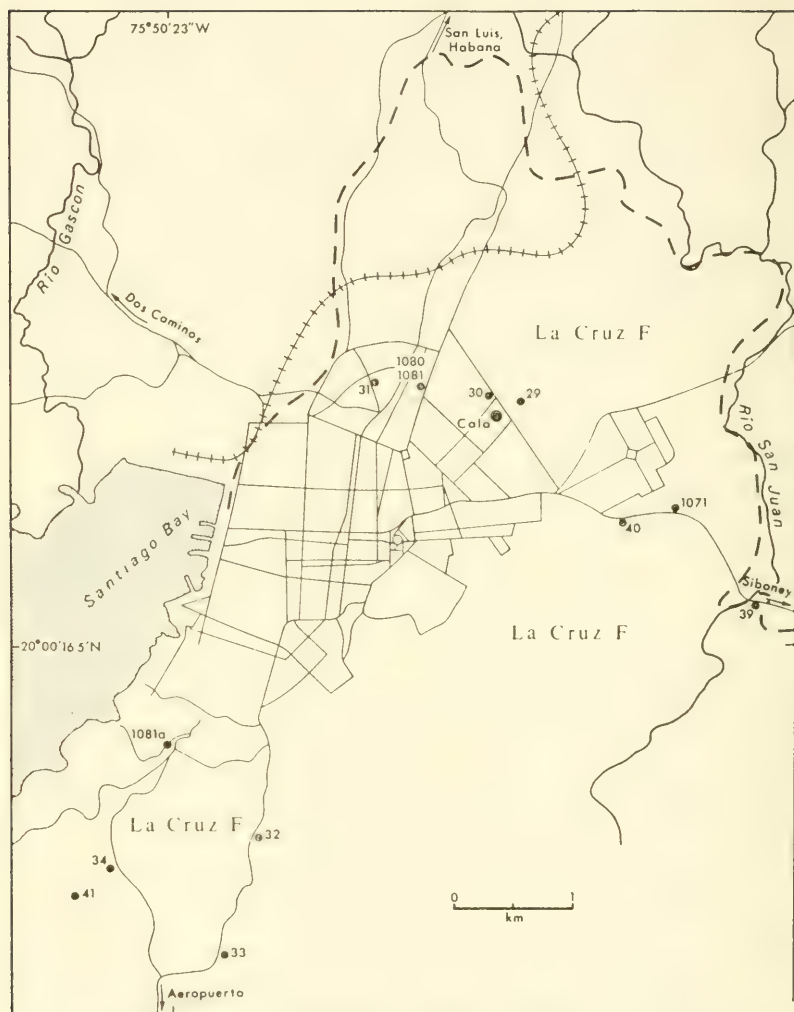
A comparison of the total La Cruz fauna of the young Neogene of Matanzas, shows 29 species in common with the total section, but only 19 with the Canímar Formation (of a total of 32 species). There are some striking similarities *e.g.* *Cyprideis bensoni*, *Radimella confragosa*, several species of *Caudites*, *Quadracythere*, *Procythereis*? and *Aurila*, *Coquimba congestocostata*, *Neocaudites triplistriatus*. But also some striking dissimilarities: In the La Cruz fauna: *Cyprideis salebrosa* and *C. subquadraregularis* and different species of *Perissocytheridea*, *Loxoconcha*, and *Paracytheridea*, absence of *Paracytheroma*. Some species are represented in the Canímar section by related ones:

La Cruz	Canímar
<i>Radimella confragosa</i> + form A	only <i>Radimella confragosa</i>
<i>Orionina serrulata</i> (Brady)	<i>Orionina vaughani</i> (Ulrich and
<i>Cytheretta ponceana</i> van den	Bassler)
Bold	<i>Cytheretta pumicosa</i> (Brady)
<i>Uroleberis torquata</i> van den	<i>Uroleberis angulata</i> (Brady)
Bold	

These species of the La Cruz Formation that are represented by related ones in the Canímar section are all species that have previously been described from Hispaniola and Puerto Rico, whereas the Canímar section species show more similarity with the Gulf Coast fauna. Another example of this is the presence of *Hulingsina* in the El Abra Formation. *Orionina vaughani* was shown in Trinidad to differentiate in the late Miocene in several species (*e.g.* *O. serrulata*), whereas in Florida it continues until the Pleistocene (van den Bold, 1963a). These differences in the fauna suggest a mixing of faunas that were originally farther separated or more specifically an encroachment of the Gulf Coast fauna upon the Antillean one, a process that is more advanced in the Recent fauna.

LOCALITIES AROUND SANTIAGO DE CUBA (Text-fig. 4)

CU 29: Escuela de Medicina, behind workers' mess in a new building project. Exposed is a 3 m thick layer of clay and sandy clay with brachiopods and bivalves. The clay is brown, yellow weathering; sands are yellow, almost white on weathering.



Text-figure 4. Location of samples in the area of Santiago de Cuba. Dashed line indicates the northern limit of the La Cruz Formation.

- CU 30: 100 m. W. of the Escuela de Medicina, outcrop on Avenide de las Américas in new housing construction: light brown sand and sandy clay with bivalves.
- CU 31: Corner of Calle Martí and Donato Mármol: two 2 ft. thick layers of sandy limestone, separated by 4 ft. of soft white marl. Sample is marl.
- CU 32: Carretera del Morro-Vista Hermosa: Grey, sandy clay, immediately below a hard bench of conglomerate, about 2 m thick.
- CU 33: Cut opposite Hotel Versailles: 10 m of almost white marl, about 30 m stratigraphically above CU 32.
- CU 34: Cement quarry S of the town. Section of fine-grained yellowish-white sands with channel-cut of fine conglomerate. Above this: massive fine-grained white calcareous sand with bivalves and brachipods. This could be the same level as CU 29.
- CU 39: A few meters above the base of the formation, to the right of the road to Siboney, just E of the bridge over the Río San Juan.
- CU 40: Parque Zoológico: Soft, sandy marl, just below thick conglomerate. Local geologists think that this is the same conglomerate as in CU 32. About 20 m higher is a soft sandy marly layer with many pebbles on which lies a soft sandy marl with *Pecten*.
- CU 41: Highest point in cement quarry, 200 m. SW of CU 34. Oysterbed over loosely cemented marly limestone blocks of irregular shape (about 3 m diam.), with at least one fossil horizon (especially *Pecten*) covered in turn by at least 20 m of weathered clay (no fossils).

In addition to these I have the fauna which came from the well in the grounds of the Escuela de Medicina, close to CU 29 and 30. It came from a soft marl at 70 cm depth.

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TAXONOMY AND DESCRIPTIONS

Subclass OSTRACODA Latreille

Order PODOCOPIDA Sars

Suborder PLATYCOPINA Sars

Family CYTHERELLIDAE Sars

	Playa de Baracoa	Bahia de Cardenas	Bahia de Matanzas	Punta Sabanilla	Costa de Matanzas	Playa de Caibarien	Cayo Piedras Cardenas	Costa Norte	Costa de Oriente
<i>Cythereella pondora</i> Kornicker									
<i>Cythereella</i> sp.									
<i>Cythereelloidea</i> forsi Puri									
<i>Cythereelloidea</i> sp.									
<i>Proponocypris</i> sp.									
<i>Paracypris</i> sp.									
<i>Macrocypris</i> sp. off. <i>M. maculata</i> (Brady)									
<i>Disoponocypris laevis</i> (Puri)									
<i>Bairdia longistotata</i> Brady									
<i>Bairdia vichix</i> Brady									
<i>Bairdia</i> sp.									
<i>Paranessidea</i> sp.									
<i>Glyptobairdia coronata</i> (Brady)									
<i>Hovanordia hovanensis</i> Pokorný									
<i>Cypriides salebrosa</i> van den Bold									
<i>Cypriides similis</i> (Brady)									
<i>Hemicypriidea?</i> <i>seipunctata</i> (Brady)									
<i>Colistocypridea</i> sp.									
<i>Munszeysella?</i> <i>inconspicua</i> (Brady)									
<i>Cuschnossidea</i> sp.									
<i>Ferissocypriidea</i> <i>bicelliforma</i> Swain									
<i>Pumilocypriidea</i> <i>subrugosa</i> (Brady)									
<i>Gongamocypriidea</i> <i>dichya</i> van den Bold									
<i>Radinella confregosa</i> (Edwards) forma A									
<i>Radinella</i> sp. 2									
<i>Radinella</i> sp. 3									
<i>Caudites angulatus</i> Puri									
<i>Caudites howei</i> Puri									
<i>Caudites nipeensis</i> van den Bold									
<i>Caudites rectangularis</i> (Brady)									
<i>Orionina</i> <i>bradyi</i> van den Bold									
<i>Palaocista</i> sp.									
<i>Coquimba</i> sp. off. <i>C. congestocista</i> (van den Bold)									
<i>Coquimba</i> sp.									
<i>Quadracythere producta</i> (Brady)									
<i>Quadracythere</i> sp. off. <i>Q. oequialis</i> (van den Bold)									
<i>Jugosocythereis pannosa</i> (Brady)									
<i>Hermionites hornibrooki</i> (Puri)									
<i>Hermionites</i> sp.									
<i>Actinocythereis bahamensis</i> (Brady)									
<i>Platycosta?</i> sp.									
<i>Neocaudites nevianii</i> Puri									
<i>Oculocythereis angusta</i> van den Bold									
<i>Proteocosta</i> sp.									
<i>Nov. gen. yoni</i> (Puri)									
<i>Cythereella pumicosa</i> (Brady)									
<i>Loxocantha fischeri</i> (Brady)									
<i>Loxocantha dorsolobulata</i> (Brady)									
<i>Loxocantha rugosa</i> van den Bold									
<i>Loxocantha ochlokanensis</i> Puri									
<i>Loxocantha levis</i> Brady									
<i>Cytheropleron</i> sp.									
<i>Paracytheridea</i> sp.									
<i>Kangaroo</i> sp. off. <i>K. abyssicola</i> (Müller)									
<i>Cytherura</i> sp. off. <i>C. johnsoni</i> Mincher									
<i>Semicytherura</i> sp.									
<i>Hemicytherura cronkekyensis</i> Puri									
<i>Hemicytherura bradyi</i> (Puri)									
<i>Xestoleberis</i> spp.									
<i>Uroleberis</i> sp.									

Table 5. Distribution of ostracodes in samples of the north coast of Cuba from Havana to Oriente.

Genus **CYTHERELLA** Jones 1849**Cytherella polita** Brady*Cytherella polita* Brady, 1869, p. 161, pl. 19, figs. 5-7.*Cytherella burcki* van den Bold, 1946, p. 59 (part), not pl. 1, figs. 1 a-e.Not *Cytherella polita* Brady, van den Bold, 1946, p. 60, pl. 3, figs. 2, a, b.*Distribution.* — Widespread in Caribbean from Miocene to Recent. Both La Cruz and Matanzas Neogene of Cuba.**Cytherella** sp.*Cytherella cubensis* van den Bold, 1946, p. 59 (part), not pl. 3, figs. 1 a-d.*Distribution.* — Confined to La Cruz Formation. *Cytherella cubensis* proper is restricted to early and middle Miocene.Suborder **PODOCOPINA** Sars 1866Superfamily **CYPRIDACEA** Baird 1845Family **PONTOCYPRIDINAE** Muller, 1894Genus **PROPONTOCYPRIS** Sylvester-Bradley, 1947**Propontocypris** sp.*Erythrocypris dreikanter* (Coryell and Fields), van den Bold, 1946, p. 63, (part), not pl. 3, fig. 3.*Propontocypris* sp., van den Bold, 1966b, pl. 1, fig. 4.*Distribution.* — Only found at T 1091A and CU 31 in the La Cruz Formation, type Canímar Formation, off Cuban north coast and in Colón Harbour (Panama).Family **PARACYPRIDAE** SarsGenus **PARACYPRIS** Sars 1866**Paracypris choctawhatcheensis** Puri*Paracypris polita* Sars, van den Bold, 1946, p. 65, pl. 1, fig. 18.Not *Paracypris polita* Sars, 1866, p. 12.*Paracypris choctawhatcheensis* Puri, 1954, p. 227, pl. 1, figs. 10-12, text-figs. 2 a, b, d; McLean, 1957, p. 70, pl. 7, figs. 2 a-d.*Distribution.* — Only in La Cruz Formation.**Paracypris** sp.*Pontocypris dactylus* (Egger), van den Bold, 1946, p. 63, pl. 3, fig. 4.Not *Bairdia dactylus* Egger, 1858, p. 7, pl. 1, fig. 7 = *Paracypris dactylus* (Egger).*Paracypris* sp., van den Bold, 1968, p. 47, pl. 2, fig. 6.*Distribution.* — La Cruz Formation, Canímar Formation, Capas de *Gypsina*, Jaimanitas Formation, and off the Cuban north coast.

Family **MACROCYPRIDIDAE** MullerGenus **MACROCYPRINA** Triebel, 1960**Macrocyprina** sp. aff. **M. maculata** (Brady)

Pl. 18, fig. 14

?Cytherideis maculata Brady, 1866, p. 367 (part?), pl. 57, figs. 12, a, b.Not *Macrocypris maculata* (Brady), Brady, 1880, p. 44, pl. 1, figs. 2, a-d.*?Macrocypris maculata* (Brady), Tressler, 1954, p. 433.Not *Macrocypris maculata* (Brady), van den Bold, 1966b, pl. 1, figs. 3, a, b.

Description. — Carapace pod-shaped, highest at 0.44 of the greatest length from anterior. Anterior end regularly rounded; dorsal margin gently arched; ventral margin slightly concave; posterior end narrowly rounded ventrally. Right valve overlapping left slightly strongest overlap anterodorsally and midventrally.

Dimensions. — L: 1.47; H: 0.54.

Remarks. — This species is similar to Brady's 1866 figures, but it cannot be determined which specimens are from Australia and which from the West Indies. Part of that species may belong to *Macrocyprina propingua* Triebel, (1960, p. 119, pl. 14, fig. 7-10; pl. 15, figs. 11-17; pl. 16, figs. 20-24; pl. 17, figs. 25-32) which is shorter and relatively higher. Cuban specimens are less acuminate behind than *Macrocypris maculata* (Brady) of van den Bold, (1966b) from Colón (Panama).

Superfamily **BAIRDIACEA** SarsFamily **BAIRDIIDAE** SarsGenus **BAIRDIA** M'Coy, 1844**Bairdia antillea** van den Bold

Pl. 15, fig. 1

Bairdia antillea van den Bold, 1946, p. 69, pl. 1, fig. 2; 1965, p. 587, pl. 1, fig. 12; 1968, p. 49, pl. 7, figs. 8, a, b; 1972b, p. 424. ? Ruggieri, 1960, p. 3; Baker and Hulings, 1966, p. 1113, pl. 1, fig. 16.

Dimensions. — L: 1.14.

Distribution. — Throughout Cuban Neogene.

Bairdia "amygdaloides" Brady

Pl. 14, fig. 9

Bairdia amygdaloides Brady, van den Bold, 1946, p. 70, pl. 1, fig. 4.

Not *Bairdia amygdaloides* Brady, 1866, p. 364, pl. 57, figs. 6 a-c.

Bairdia amygdaloides Brady, van den Bold, 1957, p. 236, pl. 1, figs. 6 a-b; 1958, table 1; 1963b, table 5; Gordon, 1961, p. 610.

Bairdia willisensis (Puri), van den Bold, 1965, p. 389, pl. 1, fig. 14, 1968, tables 4, 5, 7-10, 12.

Not *Bairdoppilata willisensis* Puri, 1954, p. 225, pl. 1, figs. 5-8, text-figs. 1 e-h.

Dimensions. — L: 1.16.

Remarks. — Both *Bairdia amygdaloides* Brady and *Bairdopilata willisensis* Puri lack the two abrupt changes of direction of the dorsal margin at the greatest height and halfway down to the posterior end; moreover the latter is distinctly smaller.

Bairdia oblongata van den Bold Pl. 14, fig. 10; Pl. 15, figs. 11, 12

Bairdia amygdaloides Brady var. *oblongata* van den Bold, 1946, p. 70, pl. 1, fig. 5.

Holotype. — A complete carapace, Univ. Utrecht, Geol. Inst. S 12972.

Paratype. — D 27040 - 27042.

Type locality. — Tschopp 1081A.

Stratigraphic horizon. — La Cruz Formation.

Dimensions. — L: 1.40.

Remarks. — In 1946 this form was separated from *Bairdia "amygdaloides"* Brady because of its more elongate shape. In fact it is not impossible that it represents the male of that species. This is the main reason why that species has not been renamed: in case it turns out to be the female of the same species as *B. oblongata*, this name should be applied, which would be unfortunate as the female of the species is squat indeed.

Bairdia sp. aff. **B. victrix** Brady Pl. 15, fig. 8

?*Bairdia victrix* Brady, Puri, 1960, p. 131, pl. 6, fig. 13; Benson and Coleman, 1963, (part), pl. 2, figs. 8-10; Hulings, 1967, p. 637, figs. 2b, 3c, d.
Not *Bairdia victrix* Brady, 1869, p. 152, pl. 18, figs. 17, 18.

Dimensions. — L: 1.06.

Remarks. — Although of the same shape as *Bairdia victrix*, this species lacks the strong anterior and posterior frills.

Bairdia laevicula Edwards Pl. 15, figs. 9, 10

Bairdia laevicula Edwards, 1944, p. 506, pl. 85, figs. 3, 4; Swain, 1951, p. 17; Puri, 1954, p. 223, pl. 1, fig. 1, text-fig. 1 d; Hall, 1965, p. 27, pl. 1, fig. 7; Baker and Hulings, 1966, p. 114, pl. 1, fig. 18; Swain, 1968, p. 7, pl. 1, figs. 4 a, b, pl. 7, fig. 2, text-fig. 5.

Dimensions. — L: 0.91.

Occurrence. — Fairly widespread in young Neogene of the Greater Antilles.

Bairdia dimorpha van den Bold Pl. 15, figs. 13-14; Pl. 15, figs. 16, 17

Bairdia timorpha van den Bold, 1963b, p. 373, pl. 1, figs. 6 a-d; 1966c, table 1.

Dimensions. — L: 0.92.

Remarks. — The ♀ female form is similar to the female form originally described from the Springvale Formation of Trinidad. The ♂ male, however, is slightly more acuminate behind than the forms originally considered as males, and are, therefore, only questionably assigned to this species (Pl. 15, figs. 16, 17).

Genus **DISOPONTOCYPRIS** Mandelstam, 1956

Disopontocypris pachyconcha (van den Bold) Pl. 14, fig. 8

Bythocypris pachyconcha van den Bold, 1946, p. 67 (part), pl. 1, fig. 11.

Bythocypris howei Puri, 1954, p. 226 (part), pl. 1, fig. 16, text-fig. 2 g (not pl. 1, figs. 14, 15, text-figs. 2 e-f).

Bythocypris keiji van den Bold, 1963b, p. 374, pl. 1, figs. 7 a-b; pl. 12, fig. 10; 1966a, tables 1, 2; 1968, tables 4, 5, 7, 9, 11, 13.

Propontocypris caboblancoensis Rodriguez, 1969, p. 169, pl. 1, figs. 5, 6, text-fig. 4.

Not *Disopontocypris pachyconcha* (van den Bold), van den Bold, 1970, p. 43, pl. 2, fig. 1.

Dimensions. — L: 1.03.

Holotype. — A complete carapace S 12967, Univ. Utrecht, Geol. Inst.

Type locality. — T 1081A.

Stratigraphic horizon. — La Cruz Formation.

Remarks. — The holotype of this species is from the La Cruz Formation, and the specimens commonly occurring in the Paso Real Formation (l-m Miocene of Cuba) have a more rounded posterior end. These were used as typical representatives of the species when material from Anguilla (van den Bold, 1970) was assigned to this species and when *Bythocypris keiji* (van den Bold, 1963b) was set up as a different species. Later comparison has shown the La Cruz and Springvale specimens to be identical and, therefore, those from the Cuban Miocene need a new name.

Superfamily **CYTHERACEA** Baird

Family **CYTHERIDEIDAE** Sars

Subfamily **NEOCYTHERIDEIDINAE** Puri

Genus **CUSHMANIDEA** Blake, 1933

Cushmanidea sp. aff. **C. howei** (van den Bold) Pl. 18, fig. 9

Dimensions. — L: 1.17; H: 0.57.

Remarks. — This species differs from *Cytherideis howei* van den Bold, 1946, p. 88, pl. 7, fig. 9) by its more compact shape and

greater curvature of the dorsal margin. In *Cushmanidea* sp. aff. *C. howei* van den Bold (1968, p. 52, pl. 4, fig. 9) this curvature is even less than in the original species. *Cytherideis ulrichi* Howe and Johnson (Howe, *et al.*, 1935, p. 16, pl. 3, figs. 11-14) and other species of *Cushmanidea* from the Gulf Coast Neogene differ by their concave ventral margin.

Subfamily **CYTHERIDEIDINAE** Sars

Tribe **CYPRIDEIDINI** Kollmann

Genus **CYPRIDEIS** Jones, 1856

Cyprideis bensoni Sandberg

Pl. 14, figs. 1-4, 11

?*Cytheridea* (*Haplocytheridea*) *stephensoni* van den Bold, 1946, p. 79 (part), not pl. 7, figs. 5 a-f = *Hemicyprideis stephensoni* (van den Bold).

?*Cytheridea* (*Haplocytheridea*) *cubensis* van den Bold, 1946, p. 79 (part), not pl. 7, figs. 1 a-e = *Hemicyprideis cubensis cubensis* (van den Bold).

Cyprideis castus Benson, Sandberg, 1964, p. 102, pl. 7, figs. 1-14; pl. 8, figs. 1-9; pl. 16, fig. 5; pl. 19, fig. 11; pl. 20, fig. 12; pl. 21, fig. 4; pl. 24, figs. 1-10.

Not *Cyprideis* (*Goerlichia*) *castus* Benson, 1959, p. 46, pl. 2, figs. 4 a-c; pl. 9, fig. 10.

Cyprideis bensoni Sandberg, 1966, p. 448; Morales, 1966, p. 30, pl. 1, figs. 1 a-b; Krutak, 1971, p. 16, pl. 1, figs. 3 a-f; van den Bold, 1974, p. 537.

Cyprideis currayi Swain, 1967, p. 50, pl. 7, figs. 11 a-c, 12.

Not *Cyprideis bensoni* Sandberg, King and Kornicker, 1970, p. 28, text-figs. 2 a, b, pl. 12, figs. 7-10.

Dimensions. — Female: L: 0.87; H: 0.49; Male: L: 0.96; H: 0.50.

Remarks. — Specimens from the La Cruz Formation are somewhat larger than typical specimens from the Recent lagoonal deposits of the Gulf of Mexico. In the La Cruz marls it is accompanied in one sample by a nodose form which is thought to be related. However, the material is recrystallized and the identification is not certain. This form has been figured as *Cyprideis bensoni* var., Plate 14, figure 11.

Distribution. — This species has been found in the late Pliocene of Costa Rica, Haiti, and Cuba. Recent distribution is from Mississippi westward along the Gulf Coast and in the southwestern Caribbean on the coast of Panama.

Cyprideis subquadraregularis (Brady)

Pl. 14, figs. 5-7

Cyprideis subquadraregularis (Brady), Sandberg, 1964, p. 162, pl. 6, figs. 9-13; van den Bold, 1969, p. 121, pl. 1, figs. 8 a-f, text-figs. 3 a-c; van den Bold, 1971, figs. 2, 4; van den Bold, 1975, p. 608.

Dimensions. — Female: L: 0.97; H: 0.59; Male: L: 0.98; H: 0.53.

Remarks. — This species was first described by Brady (1870) from the “Rade de Santiago de Cuba” and later reported to be derived in this locality by Sandberg. It has been found occurring commonly in the higher part of the La Cruz Formation in the north-eastern section of the town, but only once in the southern part.

Subfamily **PERISSOCYTHERIDEINAE** van den Bold, 1963

Genus **PERISSOCYTHERIDEA** Stephenson, 1938

Remarks. — *Perissocytheridea* appears to be a genus that is confined to tropical America. A few specimens have been described outside this region, but they do not belong to this group, except for *P. estuarina* Benson and Maddocks [1964, p. 17, text-fig. 8, (1-2), pl. 2, figs. 1-6] from Recent deposits of South Africa, which, if not to *Perissocytheridea* certainly seems to belong to the subfamily. These species have been omitted from the following list of described species:

P. alata van den Bold, l-m Miocene, Cuba, Puerto Rico, St. Croix, Anquilla, Panama. *P. anterodenticulata* Krutak, Recent, Mexico; *P. bicelliforma* Swain, Recent, Gulf Coast, ? Pliocene, Caribbean; *P. bicelliforma* var. *propsammia* Swain, Recent, Gulf Coast; *P. brachyforma* Swain, Recent, Gulf Coast; *P. costata* (Hartmann), Recent, Brasil; *P. cribosa* (Klie), Recent, Brasil; Curaçao (homonym, possibly identical to *P. bicelliforma*); *P. cytheridellaformis* Forester, Pliocene, Española; *P. dentatmarginata* (Hartmann), Recent, San Salvador; *P. gibba* (Klie), Recent, Brasil; *P. gracilis*, Stephenson, m. Miocene, Florida; *P. krommelbeini*, Pinto and Ornellas, Recent, Brasil; *P. laevis*, Benson and Coleman, Recent, Gulf Coast; *P. ? litoralensis* Rossi de Garcia, ?Miocene, Argentina, *P. matsoni* (Stephenson), l-u Miocene, Gulf Coast, ?Caribbean; *P. meyerabichi* (Hartmann), Recent, San Salvador, Pacific Coast; *P. odomensis* Swain and Brown, Cretaceous, N. Carolina (probably not a *Perissocytheridea*); *P. ? palda* (Benson), Recent, California; *P. plauta* Forester, Pliocene, Española; *P. punctata* (Hartmann), Recent, San Salvador; *P. rugata* Swain, Recent, Gulf Coast; *P. subpyriforma* Edwards, u. Miocene-Pliocene, N. Carolina; *P. subrugosa* (Brady), Recent, Pliocene, Caribbean; *P. swaini* Benson and Kaesler, Recent, Gulf of Mexico, California; *P. troglodyta* (Swain), Recent, Gulf Coast; *P. sp.* Laurencich, Oligocene, Mexico. To this list at least two species from the La Cruz Formation can be added.

Perissocytheridea pumila, n. sp.

Pl. 19, figs. 1-7

Name. — *pumilus* (L) — little, dwarfish.

Holotype. — A complete carapace of a female, HVH No. 9157.

Paratypes. — HVH No. 9158, 9159.

Type locality. — Well in the grounds of the Escuela de Medicina at the University of Oriente, Santiago, Cuba, at 0.70 m depth.

Stratigraphic horizon. — La Cruz Formation.

Description. — Female: Carapace subovate, highest at $3/7$ of the length from the anterior. Anterior end obliquely rounded, carrying 4-5 blunt spines; dorsal margin convex; ventral margin slightly sinuate, converging towards posterior; posterior end angled sub-ventrally, steep and slightly concave in dorsal part. Dorsal view lens-shaped, widest in the middle, ends rounded. Surface reticulate with irregular pattern: some ridges between rows of meshes stand out, parallel to anterior and posterior margins; a posterodorsal ridge diverges posteriorly from the dorsal margin and slightly projects over it in side view.

Male: More slender than female, highest at $7/11$ of the length from the anterior. Ventral margin almost straight. Surface more distinctly reticulate than in the female: especially the dorsal ridge is standing out and also an oblique ridge, running from the greatest height to below the middle of the anterior margin, where it connects to an irregular ridge, which meets a ventral ridge about $1/3$ of the length from the anterior. This ventral ridge ends at about $1/3$ of the length from the posterior. Dorsal view irregular, due to the projecting ridges, sides generally parallel, greatest width at about $2/3$ of the length from anterior. Sides slightly compressed laterally at $3/7$ of the length. Anterior end forms about 90° angle. Hinge and marginal area as described for the genus, muscle scars not observed.

Dimensions. — Female: L: 0.41, H: 0.27; Male: L: 0.43, H: 0.22, W: 0.20.

Remarks. — *Perissocytheridea anterodenticulata* Krutak (1971, p. 18, pl. 3, figs. 4 a-d) from the Mandinga Lagoon in Mexico is of the same general size and shape but presents weaker and different ornamentation. *P. meyerabichi* (Hartmann) (Swain, 1967, p. 53, text-figs. 4, f-i, 44 c-d; pl. 4, figs. 7 a-b, 8 a-c; pl. 8, figs. 1 a-d), is similar in outline but much larger (*Ilyocythere meyerabichi* Hartmann, 1953, p. 21, text-figs. 1-17).

***Perissocytheridea compressa*, n. sp.**

Pl. 16, figs. 7-10

Name. — *compressus* (L) — compressed.

Holotype. — Complete female carapace, HVH No. 9161.

Paratypes. — One female, 2 male carapaces, HVH No. 9160, 7 carapaces, HVH No. 9159.

Type locality. — CU 29.

Stratigraphic horizon. — La Cruz Formation.

Description. — Female: subquadrangular, highest at about $2/5$ of the length from the anterior. Anterior end obliquely rounded; dorsal and ventral margin almost straight, gently convex, almost parallel, slightly converging towards the posterior; posterior end short, bluntly angled below the middle, steeply truncate above with a slight concavity, rounded below. Dorsal view elongate ovate, widest at about 0.65 of the length from the anterior, sides convex; posterior end rounded; anterior end with a forwardly projecting, laterally compressed lip in both valves; the one in the left valve projects strongly over the left, giving the impression of a backward displacement of the right valve. Left valve larger than the right, strongest overlap at anterior end.

Surface reticulation consists of relatively large, irregular meshes, which in the anterior portion of the valve enclose smaller ones; in the centre and posterior the large meshes form rows, parallel to the venter in the ventral part, convex upward in the dorsal part. In these areas the small, secondary meshes are subdued or absent.

Male: similar to female but more elongate and with longer posterior end. A postero-dorsal swelling projects over the dorsal margin and here the carapace is actually higher (at $3/5$ of the length from the anterior) than at the anterior cardinal angle (at 0.36 of the length from the front). Posterior end has a more oblique dorsal part. Dorsal view similar to the female, but more elongate, greatest width at 0.57 of the length from the anterior. Reticulation similar to female; the convex rows of meshes follow the curve of the dorsal swelling.

Dimensions. — Female: L: 0.49 ; H: 0.31 ; W: 0.26 ; Male: L: 0.51 ; H: 0.28 ; W: 0.22 .

Remarks. — Females are similar to *P. brachyforma* Swain (1955, p. 619, pl. 61, figs. 1 a-e, 2 a-e, 5 a-g, text-fig. 39 (6 a-c)), but laterally flatter, less pointed behind and smaller and the males are more strongly different with less dorsal swelling. Also the ventral ridge of *P. brachyforma* is not developed here.

Distribution. — This species was also observed in the upper part of the Las Cahobas Formation of Haiti.

Perissocytheridea sp.

Pl. 18, figs. 5-8

Perissocytheridea matsoni (Stephenson), van den Bold, 1946, p. 84, (part), not pl. 8, figs. 9 a-b.

Description. — Female: Carapace subovate, highest at about $1/3$ of the length from anterior. Anterior end obliquely rounded; dorsal margin slightly sinuate, ventral margin almost straight in anterior $2/3$, converging towards the dorsal, posteriorly convex; posterior end blunt, angled in the middle, obliquely truncate above, rounded below. Dorsal view elongate egg-shaped, widest at $2/3$ from the anterior, sides gently converging anteriorly; both ends rounded, anterior with a slightly projecting rim in the left valve. Left valve larger than right and overlapping along dorsal and ventral margin, strongest overlap in dorsal part of posterior and anterior margin. Surface roughly punctate in central and posterior part, smooth in anterior. The punctations form rows, parallel to the posterodorsal margin with irregularly nodose ridges in between.

Male: Carapace elongate subrectangular. Anterior end blunt; dorsal and ventral margin almost straight and parallel; dorsal margin sloping down gradually into convex dorsal part of posterior end, which is rounded below the middle. Dorsal view pyriform, greatest width at $5/7$ of the length from anterior, slight lateral compression of the sides at about $1/3$ of the length.

Dimensions. — Female: L: 0.49; H: 0.30; W: 0.29; Male: 0.52; H: 0.24, W: 0.25.

Remarks. — The posterior end of this species is much blunter than in most other species of the genus and the anterior end is short. The material, however, is not well enough preserved to warrant the setting up of a new species.

Family **TRACHYLEBERIDIDAE**Subfamily **HEMICYTHERINAE**Genus **RADIMELLA** Pokorný, 1968

Species of the genus *Radimella* is discussed, Journal of Paleontology, volume 49, pages 692-701, 1975.

Radimella confragosa (Edwards)

Pl. 17, fig. 1

Hemicythere confragosa Edwards, 1944, p. 518, pl. 66, figs. 23-26.

Distribution. — Plio-Pleistocene, Caribbean. Both La Cruz and Canímar Formations.

Radimella confragosa form A

Distribution. — Pliocene-Recent, Greater Antilles, in Cuba only in Oriente Province.

Radimella sp. 2

Remarks. — This species will be described from Recent deposits on the British Honduras shelf by J. W. Teeter.

Distribution. — ? Late Pliocene, Pleistocene-Recent, Caribbean. In Cuba in Jaimanitas, Matanzas Formation, and possibly equivalent beds.

Genus AURILA Pokorný**Aurila, n. sp.**

Pl. 17, figs. 2-8

As this species will be described from British Honduras by J. W. Teeter, it will be carried here in open nomenclature.

Description. — Carapace subquadrangular to subovate in outline, highest at the anterior cardinal angle at $3/8$ of the length from the anterior; almost of equal height at a point about midway the dorsal margin, just behind the middle of the carapace. Anterior end obliquely rounded; dorsal margin parallel to ventral in its anterior half, slightly convex, and sloping down about 30° in posterior half where it is slightly concave; posterior cardinal angle very pronounced; posterior end angled below the middle, steep and concave above, rounded and bearing some obtuse spines below; ventral margin slightly sinuate, concave below the anterior cardinal angle. Surface pitted in the centre, the pits gradually becoming larger towards the periphery and forming the meshes of a reticulation: especially the meshes bordering anterior and ventral ridge and the three meshes forming the posterodorsal boss are coarse. The ridges of the reticulation follow a pattern: one set, close and parallel to the ventral margin, curves upward in anterior and posterior end, more or less paralleling the anterior margin; the other set takes an almost semicircular course, curving down in the ends. Anterior and ventral ridge belong to the first set; they both seem to lose their individuality in the strongly curved anteroventral region. Postdorsal boss variable in size, sometimes projecting sharply beyond the posterior cardinal angle (Pl. 17, fig. 4); always more pronounced in the left valve than in the right.

Dorsal view lens-shaped, widest just behind the middle; the regular curve of the sides is broken near the posterior end by the projecting posterodorsal bosses; the anterior end is stepped-down by the anterior ridge.

Hinge typical for the genus, with a restriction of the posterior tooth or socket, and a pronounced accommodation groove in the left valve. Selvage pronounced, sharply incurved midventrally in the right valve. Marginal area fairly broad with numerous radial pore-canal. Muscle-scars: six adductor scars with 1-2-2-1 vertical arrangement, three frontal scars in an oblique line and 2 mandibular scars.

Dimensions. — L: 0.69; H: 0.44; W: 0.31.

Distribution. — So far this species has been found in the La Cruz Formation, the Canimar Formation, Capas de *Gypsina*, and in Recent deposits off British Honduras.

Genus **ORIONINA** Puri, 1954

Orionina serrulata (Brady)

Cythere serrulata Brady, 1969, p. 153, pl. 18, figs. 11, 12.

Orionina serrulata (Brady), van den Bold, 1963a, p. 44, pl. 4, figs. 1-6, text-fig. 5 (6, 7, 8, a-d) with synonymy; van den Bold, 1966b, p. 47, pl. 1, fig. 8; Baker and Hulings, 1966, p. 114, pl. 1, fig. 9; van den Bold, 1967, p. 311.

?*Orionina pseudovaughani* Swain, 1967, p. 86, text-fig. 50 d-g, 54, pl. 3, figs. 5 a, b, 13; pl. 4, fig. 6 a-c; Swain, 1969, p. 468, pl. 3, fig. 2 a-d; pl. 10, fig. 1 a, b.

?*Orionina lienenklausii* (Müller), Swain, 1969, p. 468, pl. 3, fig. 2 a-c.

Distribution. — The occurrence in the La Cruz Formation is the westernmost Pliocene presence recorded of this species. In the Matanzas area the Mio-Pliocene northern American form *O. vaughani* (Ulrich and Bassler) appears to occur, but its presence could be proven without doubt in only one instance, namely in the Capas de *Gypsina*, because of recrystallization or absence of single valves, which made it impossible to examine the marginal area in detail.

Genus **CAUDITES** Coryell and Fields, 1937

Caudites sp.

Pl. 18, figs. 10, 11

Description. — Carapace subovate, highest at anterior cardinal angle, about 1/3 of the length from the anterior. Anterior end obliquely rounded, dorsal margin gently convex, ventral margin

sinuate; posterior end somewhat angled below the middle, obliquely truncate and slightly concave above, rounded below. Surface ornamented with vague and irregular ridges. One, more distinct, parallels the dorsal portion of the anterior marginal another one forms the vertical rim behind which the posterior end is laterally compressed, just in front of the posterior cardinal angle. Male more slender than the female.

Dimensions. — Female: L: 0.64; H: 0.33; Male: L: 0.66, H: 0.52.

Remarks. — There is some similarity with *Caudites medialis* Coryell and Fields as figured by van den Bold (1971, pl. 3, fig. 9) from the Pliocene of Jamaica, but the present species lacks the split median ridge near the anterior.

Subfamily TRACHYLEBERIDINAE?

Genus NEOCAUDITES Puri, 1960

Neocaudites triplistriatus (Edwards)

Pl. 17, fig. 11

Cythereis triplistriata Edwards, 1944, p. 522, pl. 87, figs. 24-28.

Not *Trachyleberis*? cf. *T?* *triplistriata* (Edwards), Swain, 1951, p. 37, pl. 6, figs. 2, 3.

Rectotrachyleberis cf. *triplistriata* (Edwards), Puri, 1954, p. 264, pl. 11, figs. 1, 2.

Neocaudites triplistriatus (Edwards), van den Bold, 1963b, p. 389, pl. 9, fig. 4.

Costa triplistriata (Edwards), Hall, 1965, p. 33, pl. 7, figs. 6, 9, 10.

Not *Neocaudites triplistriata* (Edwards), Hulings, 1967, p. 654, text-figs. 4a, 7i.

Neocaudites triplistriatus (Edwards), van den Bold, 1968, table 4, p. 29; 1971, pl. 2, fig. 11.

Dimensions. — Female: L: 0.63, H: 0.36.

Neocaudites sp.

Pl. 19, fig. 8

Dimensions. — Female: L: 0.60; H: 0.31, Male: L: 0.63, H: 0.29.

Remarks. — This species is similar to *N. triplistriatus* (Edwards), but slightly smaller and slenderer, and differs by a fine and dense punctation, near absence of an oblique median ridge and ventral ridge and the presence of a double dentation at the anterior end; the outer row of teeth projecting from the anterior rim. Both rows consist of flat, bladelike teeth, the inner row, when seen from the front exhibits a characteristic zigzag pattern.

A similar, but larger, species occurs in the Pliocene of Costa Rica, this last one will be described from Recent deposits of British Honduras by J. W. Teeter.

Genus **PROCYTHEREIS** Skogsberg, 1939 ?**Procythereis ? howei**, n. sp.

Pl. 19, figs. 11-14

Brachycythere deformis (Reuss), van den Bold, 1946, (part), p. 107, not pl. 13, fig. a-d.*Procythereis* sp., van den Bold, 1969, p. 121, pl. 2, fig. 11, text-fig. 4a.*Name.* — After the late Dr. H. V. Howe.*Holotype.* — A complete carapace, HVH No. 9141.*Paratypes.* — Left valve, and 25 complete carapaces, HVH Nos. 9142, 9143.*Type locality.* — CU 39.*Stratigraphic horizon.* — La Cruz Formation, Cuba.*Distribution.* — Matanzas? Formation, La Cruz Formation, Cuba; Ponce Formation, Puerto Rico.

Description. — Carapace almost semicircular in side view, greatest height at 0.46 of the length from the anterior. Anterior end slightly obliquely rounded, in regular continuation of the convex dorsal margin; ventral outline almost straight, ventral margin sinuate with a concavity at $3/7$ of the length from the anterior; dorsal and ventral margin converging posteriorly; posterior end blunt, angled in the middle, concave above, rounded and bearing 4-5 rounded, knoblike spines, below; posterior cardinal angle pronounced, especially in the left valve. Dorsal view bluntly arrow-shaped, greatest width at $5/7$ of the length from the anterior; at about $6/7$ of the length the posterior portion is abruptly and strongly compressed laterally.

Surface roughly pitted to vaguely reticulate; pits or meshes angular, mostly 4-6 cornered; near the anterior end they run in rows parallel to the anterior margin; forming ridges and furrows, which continue on the flattened ventral surface. Greatest width at the end of the 4th ridge.

Hinge holamphidont with a wide accommodation groove in the left valve. Marginal area moderately broad, inner margin and line of concrescence coincide; radial porecanals numerous, simple, slightly widened in the middle. Muscle-scars: a vertical row of four with at least one V-shaped frontal scar.

Dimensions. — L: 0.76; H: 0.44; W: 0.43.*Remarks.* — Species differs from *Procythereis deformis* by having the greatest height more anteriorly, instead of in the middle of

the dorsal margin; ventral ridge less strongly developed; posterior cardinal angle less pronounced and not spinose.

Family **LOXOCONCHIDAE** Sars, 1925

Genus **LOXOCONCHA** Sars, 1866

Loxochoncha sp.

Pl. 16, figs. 11, 12

Description. — Female: Carapace short, ovate, highest near the middle. Anterior end broad, obliquely rounded; dorsal margin gently convex in left valve, straight in the right; ventral margin sinuate, slightly concave in the middle; posterior end somewhat angled above the middle, concave above, broadly rounded and keeled below.

Male: Similar to female, but greatest concavity of the ventral margin lies more anteriorly and the laterally compressed ventral margin forms a wider curve towards the posterior. Dorsal view in both spindle-shaped.

Dimensions. — Female: L: 0.61; H: 0.41; W: 0.34; Male: L: 0.62; H: 0.41; W: 0.31.

Remarks. — Rather similar in shape to *Loxoconcha cyrton* van den Bold, (1963b, p. 394, pl. 8, fig. 11, a, b), but dorsal margin of left valve is less arched and it lacks a posterodorsal protuberance.

Family **CYTHERURIDAE** Müller, 1894

Subfamily **PARACYTHERIDEINAE** Puri, 1954

Genus **PARACYTHERIDEA** Müller, 1894

Paracytheridea tschoppi van den Bold

Pl. 16, figs. 3-4

Paracytheridea tschoppi van den Bold, 1946, p. 85, pl. 16, figs. 6, 7.

Paracytheridea vanwessemi van den Bold, 1946, p. 86, pl. 16, figs. 13 a, b.

Paracytheridea tschoppi van den Bold, Keij, 1954, p. 220, pl. 4, fig. 4; van den Bold, 1957, p. 245, pl. 4, fig. 7; Benson and Coleman, 1963, p. 33, pl. 3, figs. 7, 9, 10; text-figs. 20 a, b; van den Bold, 1967, p. 313; 1968, p. 76, pl. 4, figs. 8 a-d; 1972b, p. 434.

Dimensions. — L: 0.74; H: 0.36.

Outside the Caribbean this species has been reported from Indonesia by Kingma (1948, p. 74, pl. 7, fig. 12) and in the Pacific by Allison and Holden (1971, p. 191, text-figs. 17-19).

Paracytheridea sp. 1

Pl. 16, figs. 1, 2

Paracytheridea sp. van den Bold, 1971, p. 339, pl. 2, figs. 6 a-c.

Dimensions. — L: 0.85, H: 0.40.

Remarks. — This species differs from the three others by having no "hinge-ear" at the anterior cardinal angle in the left valve.

Paracytheridea spp.

Pl. 16, figs. 5, 6

Two species of *Paracytheridea* have been found only in sample CU 30; both are figured, but they have not been separated on Table 4.

Family **XESTOLEBERIDIDAE** Sars, 1926Genus **XESTOLEBERIS** Sars, 1866**Xestoleberis** sp. 1

Pl. 18, fig. 16; Pl. 16, figs. 13, 14

Xestoleberis sp. A, van den Bold, 1946, p. 120, pl. 16, figs. 17 a-d.*?Xestoleberis* sp. E., van den Bold, 1946, p. 120, pl. 8, figs. 25 a, b.*Xestoleberis* sp. 4, van den Bold, 1968, p. 79, pl. 1, figs. 6 a-d.

Dimensions. — L: 0.65; H: 0.40; W: 0.38.

Remarks. — This species exhibits some variation in size from one sample to the other.

Xestoleberis sp. 2

Pl. 18, figs. 1-4

?Xestoleberis sp. 2, van den Bold, 1968, p. 78, pl. 6, fig. 8 a-d.

Description. — Carapace of the female roundly triangular in side view, highest at 9/16 of the length from the anterior. Anterior end low, obliquely rounded, narrowly rounded subventrally, dorsal margin arched; ventral margin slightly concave, almost straight; posterior end broad, obliquely rounded. Dorsal view egg-shaped, widest at 11/16 of the length from the anterior; anterior end narrow, somewhat pointed; posterior end broad, almost semicircular.

Male: Carapace almost semicircular in side view, highest just behind the middle, ends subequal, obliquely rounded, narrowly rounded subventrally. Dorsal view ovate, widest just behind the middle, ends subequal, anterior one somewhat pointed as in the female, the posterior one more narrowly rounded.

Dimensions. — Female: L: 0.64; H: 0.43; W: 0.49; Male: L: 0.57, H: 0.36; W: 0.37.

Remarks. — The male is similar to *Xestoleberis* sp. 2, from the Dominican Republic, but the female was not described from there and cannot be identified with any of the other three species of *Xestoleberis* reported from there. Therefore, the determination remains questionable.

Xestoleberis sp. 3

Pl. 18, figs. 15, 17

Description. — Carapace subovate, highest in the middle. Anterior end obliquely rounded, dorsal margin gently arched; ventral

margin almost straight, slightly sinuate, continuing in an upward bend into the posterior end, which is more narrowly rounded just below the middle and obliquely truncate in the dorsal part. Dorsal view elliptical, widest in the middle, anterior end rather strongly compressed laterally; posterior end rounded.

Dimensions. — L: 0.60; H: 0.37; W: 0.32.

Genus **UROLEBERIS** Triebel, 1958

***Uroleberis triangula* van den Bold**

Uroleberis triangula van den Bold, 1968, p. 80, pl. 6, fig. 5 a-c; pl. 10, fig. 1, a, b.

Remarks. — The figured specimen is slightly anomalous, being larger, more regularly rounded dorsally than other specimens and it may belong to a different species (Pl. 18, fig. 12). Other specimens are identical to the types from the Dominican Republic.

***Uroleberis torquata* van den Bold**

Uroleberis torquata van den Bold, 1968, p. 81, pl. 6, fig. 4; pl. 10, fig. 2.

Remarks. — Only a few specimens assignable to this species occur in the La Cruz Formation. Others, which are less angular have been assigned to *Uroleberis* sp.

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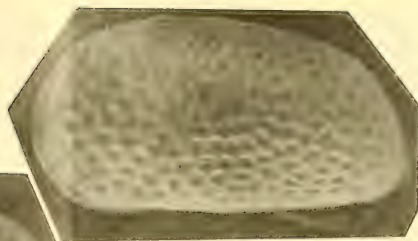
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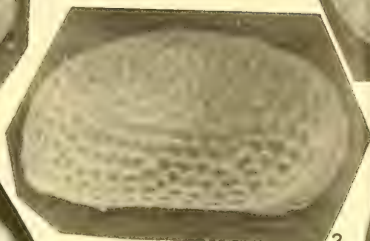
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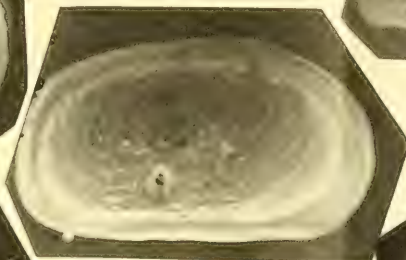
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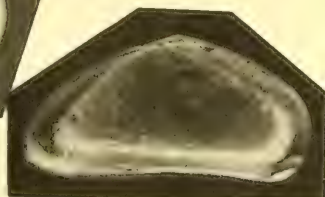
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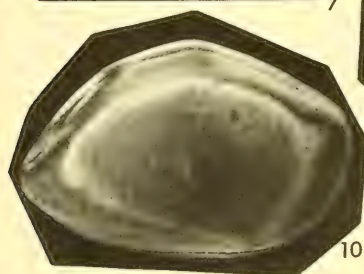
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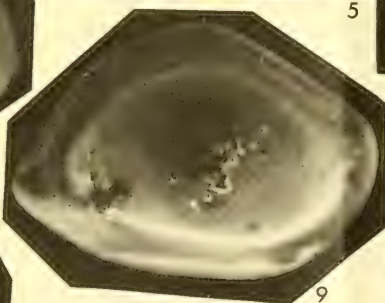
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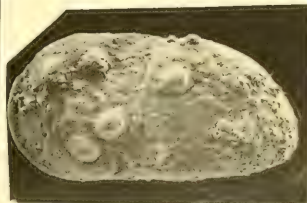
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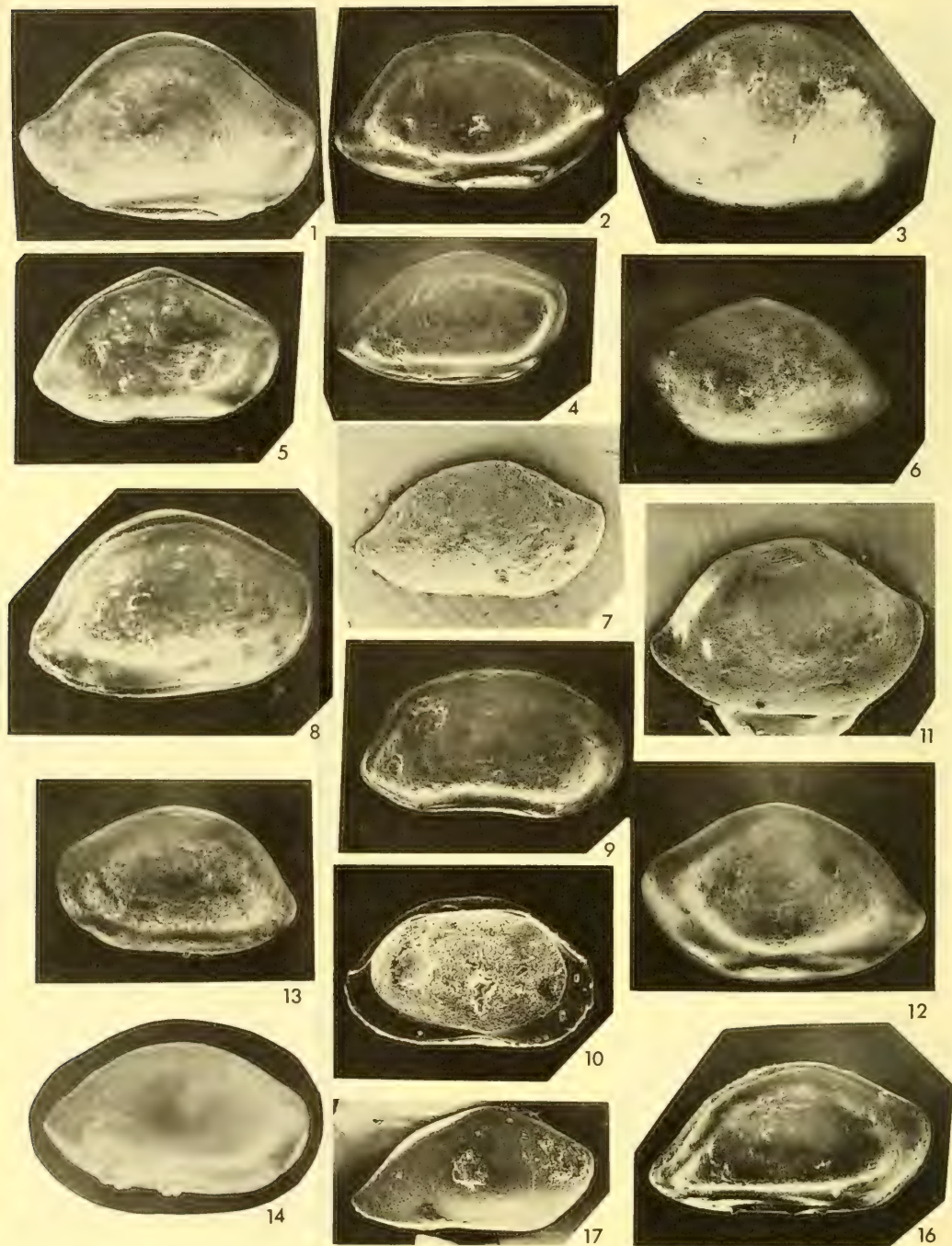
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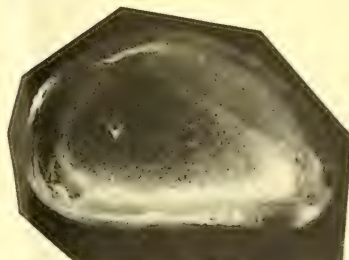
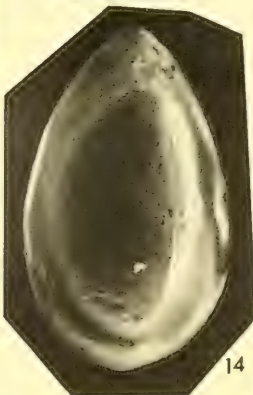
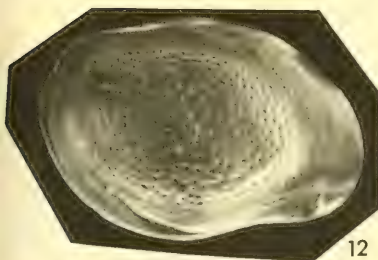
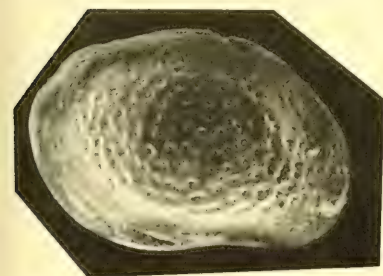
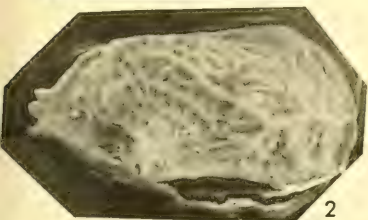
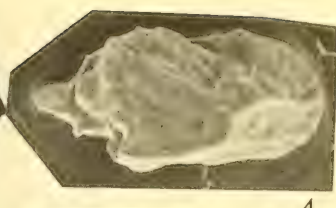
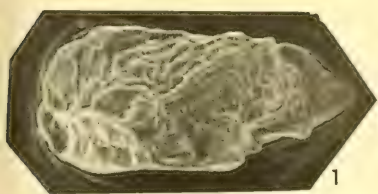


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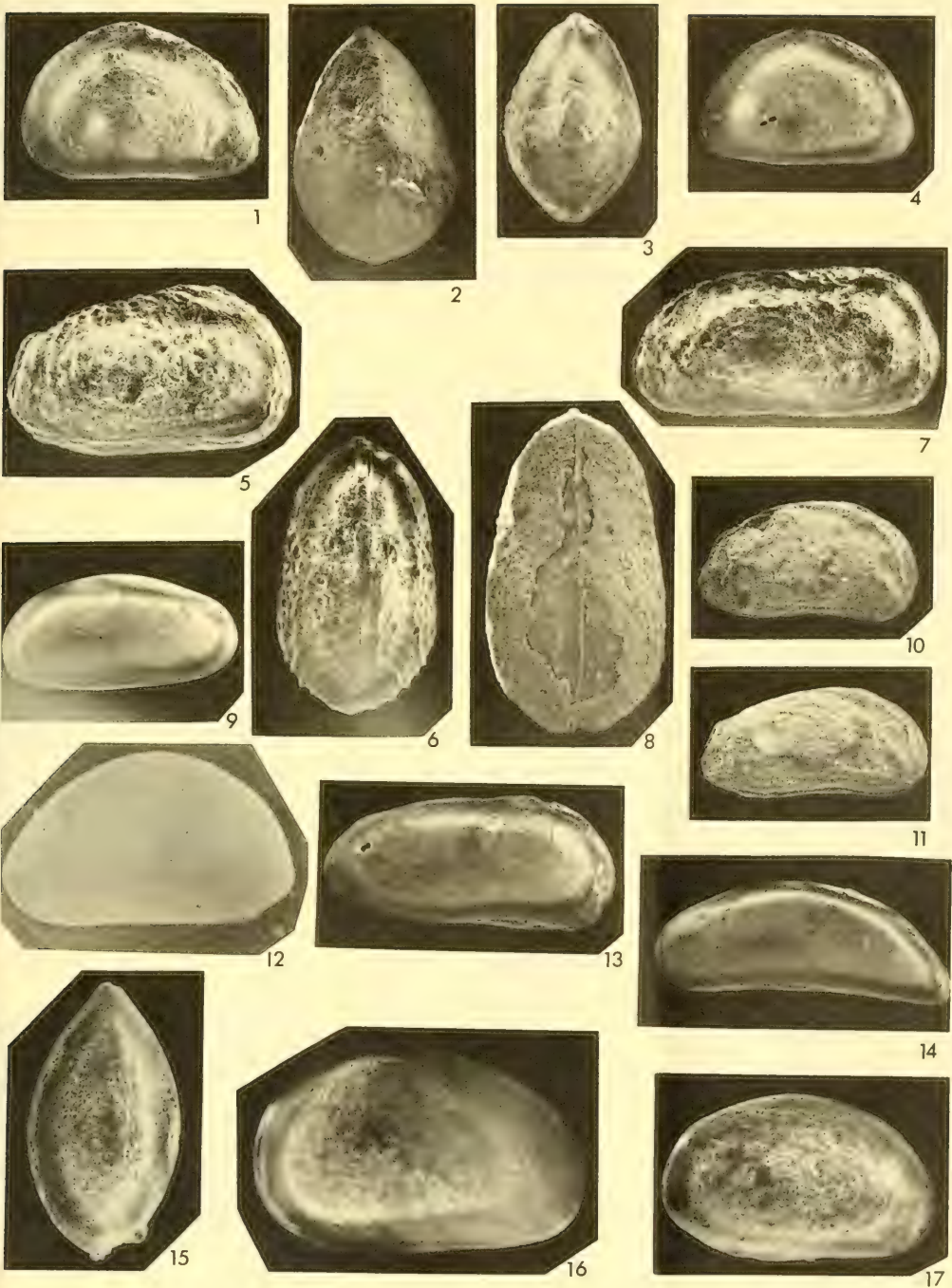


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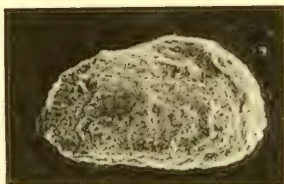
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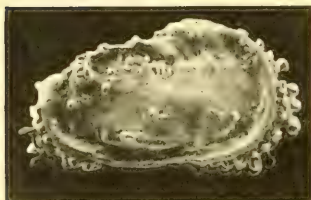
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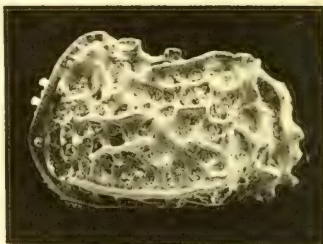
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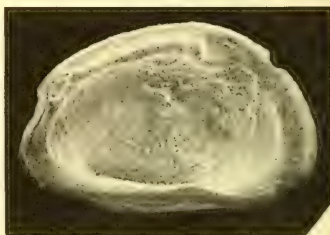
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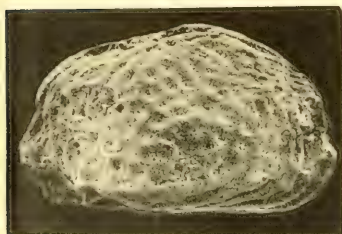
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WATERS (ACROTHORACICA
AND RHIZOCEPHALA)

By

NORMAN E. WEISBORD

1975

Paleontological Research Institution
Ithaca, New York 14850 U. S. A.

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CIRRIPIEDIA OF FLORIDA AND SURROUNDING WATERS (ACROTHORACICA AND RHIZOCEPHALA)

NORMAN E. WEISBORD

Department of Geology
The Florida State University

ABSTRACT

This report is based largely on a study of the literature. It deals with the Acrothoracica (burrowing barnacles) and Rhizocephala (parasitic barnacles) occurring in Florida and the adjacent waters of the Gulf of Mexico, the Caribbean Sea, and the Western Atlantic Ocean. Reported within this region are 4 species of Acrothoracica and 25 species of Rhizocephala. Each barnacle is briefly described, and the type illustrated from its original source. Information concerning the latitudinal range and ecological habitat of all of the discussed species is provided, and the names currently used are applied to the Decapod Crustacea infested by the rhizocephalan parasites.

Fossilization of the Acrothoracica and Rhizocephala is extremely rare because of their soft bodies. However, as determined from the character of their burrows, acrothoracicans have been discovered in the Mio-Pliocene and Pleistocene of Florida. And, as conjectured from the stratigraphic position of its host, at least one species of Rhizocephala may have existed during the late Miocene in Virginia and during the Pleistocene in Maryland.

INTRODUCTION

The work submitted herewith is a compendium which deals with the burrowing barnacles (Acrothoracica) and parasitic barnacles (Rhizocephala) occurring in Florida and in the waters surrounding it. Most of the information contained in this report has been culled from the writings of a number of authors who have provided the knowledge of, and expertise concerning these particular organisms. Unless otherwise noted therefore, the names given to cirriped species and to the hosts with which they are associated, are the same in this paper as they were in the original presentation by the author concerned.

The State of Florida is uniquely situated in that it projects into and borders upon three major bodies of water: the Gulf of Mexico, The Caribbean Sea, and the Western Atlantic Ocean. Because these waters commingle and affect each other in important respects today as well as they did during late Cenozoic time, Florida partakes geologically and faunally of temperate, semitropical, and tropical marine conditions. The result is that many of the taxa discussed in this work which are found in Florida have also been reported from latitudes far to the north and south. Conversely, it is anticipated, because of the hosts they occupy, that some of the burrowing or parasitic Cirripedia not yet reported from Florida but which occur elsewhere in the Gulf, Caribbean, or Western Atlantic, will eventually be discovered in the Floridan province.

Described are 29 species, 4 of them belonging to the order Acro-

thoracica, and 25 to the order Rhizocephala. The types of the species are illustrated, these illustrations having been reproduced from the original drawings with certain scale adjustments or modifications in their explanations. The unfigured species is *Peltogaster* sp. H. W. Wells.

The acrothoracican barnacles, which are world-wide in distribution, burrow into a variety of taxa with a calcareous skeleton, including such diverse groups as mollusks, bryozoans, serpulid polychaetes, corals, and even other barnacles. The rhizocephalan barnacles on the other hand, are parasitic only on crabs, although the same species of parasite may occur on different species of the decapod Crustacea. Thus the Floridan parasite *Briarosaccus callosus* Boschma has been found on five different species of crabs, one or the other of which occurs as far north as Alaska and as far south as the southern tip of Chile. Another Florida rhizocephalan, *Loxothylacus panopaei* (Gissler) attaches itself to eight different species of crabs whose range in the Western Atlantic extends from Massachusetts to Brazil, and in the Eastern Pacific from Alaska to California.

The slits and cavities produced by acrothoracican barnacles, generally in dead shelly material and occasionally in rock, probably causes the surface of the host to break down a little sooner than it would otherwise, but the ecological impact is minor insofar as disintegration of the shell or substrate is concerned. The adverse economic impact of some rhizocephalan parasites, however, is considerable. The parasites attach themselves to the abdomen of crabs and are nourished by the stomach contents of these hosts. This form of parasitism in the host is accompanied by degeneration of the sexual organs in both sexes and leads to sterility of the infested crabs. The edible blue crab of Gulf and Atlantic waters and the king crab of Alaskan and Eastern Pacific waters are often infested with parasites thereby diminishing the ultimate catch of this important food source for man. Considerable research on the effects of rhizocephalan parasitism was reported upon as early as 1906 by Eugene Smith and as recently as 1970 by McMullen and Yoshihara who wrote that 70 per cent of the king crabs collected in a randomly selected area off Alaska were infested with the rhizocephalan parasite *Briarosaccus callosus* Boschma.

The acrothoracican barnacles are soft-bodied animals which bur-

row into shells or calcareous substrates for protection. The burrows are formed by abrasion from the microscopic chitinous teeth distributed over the surface of the mantle. The burrow of each particular species is distinctive both in the character of the apertural slit (which is generally pointed at one end), and by the shape, depth, and orientation of the excavation which encases it. Under very unusual circumstances it is perhaps possible that the soft matter of an acrothoracican species can be preserved and identified specifically in its fossil state, but by and large fossil acrothoracicans are recognized and classified by the burrows themselves. In Florida such fossil burrows have been identified by Tomlinson and by Ross in the skeletal substance of taxa which are known to range from Miocene to Pleistocene.

Shortly after attachment, the rhizocephalan barnacle first punctures the stomach of its host crab and then is nourished by the contents to become an inflated, chitinous sac. Again, preservation of the parasite itself to endure as a recognizable fossil is again unlikely. Crabs, however, are known far back in geologic time because of the fossilization and imprint of their hard parts. An example is the modern and edible blue crab *Callinectes sapidus* Rathbun, on which the rhizocephalan parasite *Loxothylacus texanus* Boschma is adherent. *C. sapidus* is known in the present waters of the Gulf of Mexico, the Caribbean Sea, and the Western Atlantic from Nova Scotia on the north to as far south as Uruguay. *C. sapidus* has also been identified in the Miocene of Virginia and in the Pleistocene Talbot Formation of Maryland, but whether it was infested with the same rhizocephalan then as it is today can only be conjectured.

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National Museum of Natural History, for checking and confirming the authenticity of the names of the decapod crustaceans used in this work; and Katherine V. W. Palmer and staff of the Paleontological Research Institution for the editing and preparation involved in publication.

LIST OF SPECIES

The species of Acrothoracica and Rhizocephala discussed in this work are listed below. Conjoined with the Rhizocephala are the species of decapod hosts on which they are parasitic, and the latitudinal range of the hosts.

ACROTHORACICA

Lithoglyptes spinatus Tomlinson and Newman
Kochlorine floridana H. W. Wells and Tomlinson
Weltneria hessleri Newman
Trypetesa lampas (Hancock)

RHIZOCEPHALA	Rhizocephalan hosts	Latitudinal range of hosts
<i>Briarosaccus callosus</i> Boschma	<i>Paralithodes camtschaticus</i> <i>Lithodes aequispinus</i> <i>Lithodes agassizii</i>	58°24'N, Auke Bay, Alaska Bering Sea Off NE and SE coast of U.S.
	<i>Lithodes antarcticus</i>	Argentina, South Georgia, and Falkland Islands
	<i>Paralomis granulosa</i>	53°10'S, Punta Arenas, Chile
<i>Tortugaster fistulatus</i> Reinhard	<i>Munidopsis robusta</i>	Dry Tortugas, Florida
<i>Peltogaster</i> sp. H. W. Wells	<i>Pagurus longicarpus</i>	Nova Scotia to Brazil
<i>Sacculina americana</i> Reinhard	<i>Trachycarcinus spinulifer</i>	Northern Gulf of Mexico
<i>Sacculina bicuspidata</i> Boschma	<i>Microphrys bicornutus</i>	North Carolina to Brazil
<i>Sacculina boschmai</i> Reinhard	<i>Acanthocarpus alexandri</i>	Massachusetts to Grenadines
<i>Sacculina hirsuta</i> Boschma	<i>Pilumnus caribaeus</i> <i>Pilumnus dasypodus</i>	Florida Keys to Brazil North Carolina to Brazil
<i>Sacculina pustulata</i> Boschma	<i>Hemus cristulipes</i>	Northern Gulf of Mexico to Curaçao
<i>Sacculina rathbunae</i> Boschma	<i>Arachnopsis filipes</i> <i>Stenorhynchus seticornis</i>	North Carolina to Brazil Florida to Barbados

<i>Sacculina reniformis</i> Boschma	<i>Podochela riisei</i> <i>Collodes leptocheles</i>	North Carolina to Brazil Northern Gulf of Mexico to Puerto Rico
<i>Sacculina schmittii</i> Boschma	<i>Anomalothir furcillatus</i>	North Carolina to Grenada
<i>Sacculina tessellata</i> Boschma	<i>Mithrax (Mithraculus)</i> <i>ruber</i>	Cuba to Barbados
<i>Heterosaccus occi-</i> <i>dentalis</i> (Boschma)	<i>Mithrax (Mithraculus)</i> <i>forceps</i>	Bermuda; North Carolina to Brazil
	<i>Mithrax (Mithraculus)</i> <i>sculptus</i>	Florida to Brazil
	<i>Macrocoeloma</i> <i>diplacanthum</i>	Florida to Curaçao
	<i>Macrocoeloma campto-</i> <i>cerum</i>	North Carolina and Florida
	<i>Pitho anisodon</i> (von Martens)	Florida to Curaçao
	<i>Pitho iherminieri</i>	North Carolina to Brazil
	<i>Stenocionops furcata</i>	Georgia to Barbados
	<i>Microphrys bicornutus</i>	North Carolina to Brazil
<i>Loxothylacus bicorni-</i> <i>ger</i> Boschma	<i>Portunus ventralis</i>	Georgia to Cabo Frio, Bra- zil (31°N to 22°51'S)
<i>Loxothylacus engeli</i> Boschma	<i>Anasimus latus</i>	South Carolina to Trinidad
<i>Loxothylacus longi-</i> <i>pilus</i> (Boschma)	<i>Micropanope lobifrons</i>	Florida to Panama
<i>Loxothylacus panopaei</i> (Gissler)	<i>Panopeus herbstii</i>	Massachusetts to Brazil
	<i>Panopeus occidentalis</i>	North Carolina to Brazil
	<i>Eurypanopeus depressus</i>	Bermuda; Massachusetts to Florida
	<i>Pilumnus sayi</i>	North Carolina to Bahamas
	<i>Tetraxanthus rathbunae</i>	Northern Gulf of Mexico
	<i>Rithropanopeus harrisi</i>	Maine to Vera Cruz, Mexico
	<i>Tetraplax quadridentata</i>	Venezuela
	<i>Lophopanopeus bellus</i>	Eastern Pacific: Alaska to California
<i>Loxothylacus perar-</i> <i>matus</i> Reinhard and Reischman	<i>Parthenope (Platylambrus)</i> <i>pourtalesii</i>	Massachusetts to Cuba
<i>Loxothylacus texanus</i> Boschma	<i>Callinectes sapidus</i> <i>Callinectes marginatus</i>	Nova Scotia to Uruguay Bahamas to Brazil. Cape Verde Islands and West Africa
<i>Ptychascus glaber</i> Boschma	<i>Aratus pisonii</i> <i>Sesarma (Holometopus)</i> <i>benedicti</i>	Florida to Brazil Southern Florida to Rio de Janeiro, Brazil

	<i>Sesarma (Holometopus)? miersii</i>	Bahamas to Florianópolis, Brazil
<i>Lernaeodiscus bilobatus</i> Boschma	<i>Petrolisthes amoenus</i>	Cuba to Barbados
<i>Lernaeodiscus crenatus</i> Boschma	<i>Petrolisthes marginatus</i>	Puerto Rico to Tobago in Caribbean; Mexico to Ecuador in Eastern Pacific
<i>Lernaeodiscus porcellanae</i> Müller	<i>Petrolisthes galathinus</i>	North Carolina to Brazil off East America; Costa Rica to Ecuador in Eastern Pacific
	<i>Petrolisthes eriomerus</i>	La Jolla, California
<i>Lernaeodiscus schmitti</i> Reinhard	<i>Munida iris</i>	Dry Tortugas, Florida
<i>Thompsonia cubensis</i> Reinhard and Stewart	<i>Munida stimpsoni</i>	Northwest Cuba to Recife, Brazil

DESCRIPTION OF SPECIES

Order ACROTHORACICA Gruvel, 1905, p. 310

Family LITHOGLYPTIDAE Aurivillius, 1892, p. 133

Lithoglyptes spinatus Tomlinson and Newman = **Lithoglyptes bicornis** Aurivillius Pl. 20, fig. 1

Lithoglyptes spinatus Tomlinson and Newman, 1960, pp. 519-526, figs. 1-10; Ross, 1965, pp. 317-318, pl. XIII; Tomlinson, 1969a, pp. 11, 48-50, 55, 58, 143, 150, fig. 7; 1973, pp. 264, 265; Newman and Tomlinson, 1974, pp. 204-208.

Lithoglyptes bicornis Aurivillius, 1892, p. 134; 1894, p. 70, pl. V, fig. 15; Newman and Tomlinson, 1974, pp. 204-208, figs. 1, 2.

Lithoglyptes ampulla Aurivillius, 1892, p. 134; 1894, p. 71, pl. V, fig. 14; Newman and Tomlinson, 1974, pp. 204-208, figs. 1, 2.

The holotype of the burrowing cirriped *Lithoglyptes spinatus* from Jamaica was a female measuring 1.92×1.28 mm, with the aperture half representing the greatest width of the mantle. The species is obovate in lateral aspect and slightly arched, and is equipped with one pair of strong hooks and one pair of bristle-bearing spines. The anterior and posterior rami of the mouth cirri are composed of five and four articles, respectively. The caudal appendage consists of two distinct segments. The lateral bar is weak or absent. Larvae are retained until the cypris stage.

Measurements on 12 adults ranged from 1.3 mm to 2.84 mm from the basal end of the body to the middle of the rounded apertural hooks, and from 0.94 mm to 1.86 mm from the muscle attachment knob to the opposite side of the mantle. The attachment disc

adheres strongly to the burrow, and between the disc and the aperture there is a small duct opening to the exterior from what is believed to be a cement gland.

Type locality. — Salt Gut, Jamaica. The type specimen was associated with the barnacle *Lithotrya* on about 6 square inches of the dead, algae-incrusted coral *Acropora palmata* (Lamarck).

Other localities. — As indicated by Tomlinson (1969, 1973), *Lithoglyptes spinatus* is widely distributed, as follows: Bahama Islands, on *Acropora cervicornis* (Lamarck) and *Porites porites* (Pallas). Panama (Colon, 9°21'N, 79°54'W), on coral. Entedebir Island (15°43'N, 39°54'E), Landing Bay, Ethiopia, off the south coast of the Red Sea on the west of the Dahlak Archipelago. Princess Charlotte Bay, Queensland, Australia. Great Barrier Reef, Australia, in the coral *Dendrophyllia axifuga* Edwards and Haime. Heron Island (23°25'S, 151°55'E), Great Barrier Reef, in the giant pelecypod *Tridacna maxima*. Minnie Waters, near Grafton (29°40'S, 152°56'E), New South Wales, Australia, on unidentified coral in intertidal rock pools. Maldiv Islands, Indian Ocean, from coral. Jarvis Island (0°22'S, 160°3'W), Central Pacific, in *Tridacna maxima*. Sanding Island (3°29'S, 100°44'E), off west coast of Sumatra, Indonesia, on coral. Christmas Island (10°30'S, 105°40'E), Indian Ocean, in *Tridacna maxima*. Pulau Melila (2°15'N, 97°25'E), off Sumatra, Indonesia. South of Ujung Batu, Banyak Islands, 2°10'N, 97°16'E, off Sumatra. Namu Island, Bikini Atoll. East of Rigili Island, Eniwetok (11°30'N, 162°15'E), on *Turbo marmorostoma argyrostoma*. Kwajalein (8°43'N, 167°44'E), Marshall Islands, in dead coral rock. Howland Island (0°48'N, 176°38'W), Western Pacific, in *Tridacna maxima*. Burrock Island, Rongelap Atoll (11°30'N, 166°45'E). Tuamotu Archipelago (Maiai Island). Moorea, Oceania. Seto Bay and Susami Bay, Japan, in the coral *Acropora studieri*. Kuredo Island, from coral.

The distribution of *Lithoglyptes spinatus* as given above is based on the works of Tomlinson and Newman (1960) and Tomlinson (1969, 1973). However, in their most recent paper, Newman and Tomlinson (1974) now consider the Caribbean *L. spinatus* to be synonymous with *L. bicornis* Aurivillius (1892, p. 134; 1894, p. 70, pl. V, fig. 15, and with *L. ampulla* Aurivillius (1892, p. 134; 1894, p. 71, pl. V, fig. 14). The latter two species, both reported by Auri-

villius from the Java Sea, and both found burrowed in coral, are believed by Newman and Tomlinson, on morphological grounds and statistical analysis, to be developmental stages of the same species. On the other hand, and for what seem to me to be excellent reasons, Newman and Tomlinson found it difficult wholly to accept their own diagnosis of uniting the Caribbean *L. spinatus* with the Pacific *L. bicornis* on anatomical similarity alone. Taking the cue from those authors, would it not be reasonable then to consider the "Caribbean" *L. spinatus* a valid geographic or allopatric taxon?

There are only three reports of *Lithoglyptes spinatus* in the seas around Florida, and these are in the nearby Bahama Islands in the Western Atlantic, and in the Caribbean Sea off Jamaica and Panama. Inasmuch, however, as *L. spinatus* is associated with the coral *Acropora palmata*, which ranges from Florida to the north coast of South America and is found in the Pleistocene of Florida, it is anticipated that *L. spinatus* will eventually be discovered in the territorial waters of Florida itself. And, as intimated by Ross (1965), but not yet substantiated, it may also be found as a fossil, identifiable by the character of the burrow apertures, in Florida and elsewhere.

Kochlorine floridana Wells and Tomlinson

Pl. 20, figs. 2, 3

Alciippe lampas Wells [not of Hancock, 1849], 1961, p. 248 = *Kochlorine floridana* Wells and Tomlinson, 1966, *vide* Wells and Tomlinson, 1966, p. 28.

Kochlorine floridana Wells and Tomlinson, 1966, pp. 27-37, figs. 1-3; Tomlinson, 1969a, pp. 71-77, 150, fig. 15.

The body, which is enclosed in a mantle, is compressed and sac-shaped, and is slightly asymmetrical, with the posterior end somewhat twisted to the side. The mantle surface bears scattered small bi- or tricusate hooks, a little more numerous near the attachment site of males. There is a series of larger tack-shaped teeth around the margin of the aperture. The aperture is gently arched, bearing a pair of short blunt spines, usually studded with strong teeth. The length of the aperture is 0.4 to 0.8 times the body width, proportionally larger in the smallest specimens. The apertural rim and spines are ornamented by three rows of heavy teeth, the teeth in the outer row bifid, those in the inner two rows broad and tack-shaped. There is a comblike row of spinules guarding the inner edge of the aperture at the ventral end, and there is a rounded spinous knob at

the dorsal end of the aperture. The head is rounded and bears one or more rows of fine hairs. A lateral bar, finely reticulated on each side, extends posteriorly from the apertural margin. The attachment process is moderately developed. The body normally is lodged in the surrounding shell by projection of the attachment process into a small depression in the burrow wall.

The excavation produced in shell material is smooth-walled and somewhat variable, corresponding to the shape and size of the inhabitants. The excavation slants obliquely in a dorsal direction. The orifice is a narrow slit in surface view, broader at the ventral end, and considerably shorter than the maximum height of the burrow. A delicate ridge composed of opaque calcium carbonate may be built up around the orifice edge, particularly at the narrow dorsal end. The body of the male *K. floridana* is lobate and attaches itself to the wall of a burrow occupied by a female, or to the mantle of the female itself. At the type locality *K. floridana* is an abundant inhabitant of calcareous shell material, with burrows having been found in mollusks, bryozoans, serpulid polychaetes, barnacles, and corals. The length of the holotype was 2.1 mm, the width 1.125 mm, and the thickness 0.75 mm. In a series of 18 additional females, the length ranged from 0.53 to 3.33 mm and the body width 0.52 to 0.70 times the body length.

Type locality. — Gulf of Mexico, 8 miles southeast of Carabelle, Franklin County, Florida, depth 8-10 fathoms. The holotype, a female, U.S.N.M. 113221, with one attached male, was collected 16 May 1963.

Additional Florida localities. — Fernandina Beach, from *Arca imbricata* (Bruguère) and off St. Augustine, from *Murex fulvescens* G. B. Sowerby II, both along the east coast. Along the west and south coast, *Kochlorine floridana* is reported off Sarasota; off Cape St. George, from *Aequipecten gibbus* (Linnaeus); St. Andrews Bay entrance, from *Murex fulvescens*; Santa Rosa Sound, from *Crassostrea virginica* (Gmelin), and southeast of Pensacola, from the bryozoan *Hippoporida edax* (Busk).

Other localities. — North Carolina (Shackleford Banks, from *Murex fulvescens*; Back Sound, from shelly bottom; Bogue Sound; Morehead City, from shell fragments; Beaufort area; Diamond Shoals, from *Murex fulvescens* and *Cassis madagascariensis*

Lamarck; Cape Lookout jetty). South Carolina (off Charleston, from *Arca zebra* (Swainson). Georgia (off Sapelo Island; east of Brunswick, 31°19'N, 80°33'W, in 14.5-15.5 fathoms, from *Murex fulvescens*). Mississippi (Pascagoula Fishery Station). Puerto Rico, from dead coral fragments. Venezuela (east off mouth of the Orinoco River at 07°58'N, 58°23'W, in 10-11 fathoms, from *Murex pomum* Gmelin, and at 08°06'N, 58°20'W, from *Cymatium parthenopeum* von Salis). Malagasy Republic (Tuléar, 23°20'S, 43°41'E, from *Murex microphyllus* Lamarck).

In a letter dated 13 November 1974, Jack T. Tomlinson of California State University, San Francisco, informed me that two of the specimens illustrated in my paper on the late Cenozoic corals of South Florida (Weisbord, 1974), contain slits of what appeared to him to be acrothoracican barnacles, possibly "*Kochlorine floridana* or some other species." One of the corals is *Siderastrea pliocenica* Vaughan and is Pliocene to Pleistocene in age; the other is *Septastrea crassa* (Holmes), and this ranges from Mio-Pliocene to Pleistocene. Neither of the corals is known to be living, and the presence in these fossil corals of acrothoracican barnacles again suggests that these burrowing organisms may turn out to be important biostratigraphic markers.

***Weltneria hessleri* Newman**

Pl. 28, figs. 1-3

Weltneria hessleri Newman, 1971, Journal of Zoology, vol. 165, pt. 4, pp. 423-429, text-figs. 1-2, pl. I; 1974, pp. 449, 450, 452, 453, 455.

Newman's description of this species was based on six female specimens and numerous burrows in the chalk substrate. The species is the largest known pygophoran, one specimen measuring 14 mm from the bottom of the sac to the apex of the opercular bars. The burrows are perpendicular to the surface of the chalk, and their apertures oval and pointed at the carinal end. The apertures range from 3 mm to 6 mm in length, and the burrows from 5.5 mm to 10 mm in depth.

The rostral end of the body chamber in empty burrows often contains a slightly curved calcitic plate held in place by calcareous cement. These rostral plates range from 3.5 mm to 7.3 mm in height, 1.9 mm to over 2.3 mm in width, and 2.6 mm to 5.3 mm in depth. The plate has three principal parts: an open basal portion to which

the body of the barnacle is attached; a grooved side lying free of but adjacent to the body; and an outer surface cemented to the burrow. The groove runs from the basal portion to the tip or umbo, and the rostral ends of the opercular bars ride in the groove. Each opercular bar is simple and hemi-lanceolate, is without large spines or hooks, and is composed of chiton and some calcareous material.

The surface of the mantle of the female is smooth, and there is no suggestion of a lateral bar. The labrum is bullate, the crest supporting a single row of generally paired, minute teeth. Usually the mandible has five teeth but the number and arrangement are variable. The first and second maxillae are like those of other lithoglyptids.

The mouth cirri are remarkably well developed. The rami are well formed, without fused articles. The number of articles is about double that known for any other lithoglyptid, and are densely covered with plumose setae. The posterior or terminal five pairs of cirri are exceptionally long and numerous segmented. In contrast, the caudal appendages are short, consisting of two stout segments supporting numerous plumose setae, the number increasing regularly from 7 to 9 in cirrus I to 78 to 82 in cirrus VI.

Type locality. — East of Bermuda at 32°21.3'N, 64°31'W, depth about 1000 meters, bottom of foraminiferal chalk recovered from anchor dredge. Holotype, British Museum (Natural History), Reg. No. 1971.3.1,1. Paratype, U.S. National Museum of Natural History, Cat. No. 137178.

Although Bermuda is as yet the only locality reported for *Weltneria hessleri*, the species is included in this work because of the possibility it may be found in Bahaman and Floridan waters with similar depths and chalky bottom sediment near the outer edge of the continental shelf.

Family **TRYPETESIDAE** Krüger, 1940, p. 454

Trypetesa lampas (Hancock)

Pl. 20, figs. 4, 5

Alcippe lampas Hancock, 1849, pp. 313-314, pls. 8-9; Darwin, 1854, pp. 530-563, pl. 22, figs. 1-15, pl. 33, figs. 16-19; Hoek, 1876, p. 55; 1883, pp. 3, 29; Weltner, 1897b, p. 238; 1897a, p. 446; 1898, pp. 10, 13; Aurivillius, 1894, pp. 72, 75-78, 81, 82, pl. 6, figs. 1, 5-9, pl. 7, figs. 7-21, pl. 9, figs. 4, 9; Berndt, 1903, pp. 396-457, pls. 19-22; Gruvel, 1905, pp. 324-328, figs. 336-339; Genthe, 1905, pp. 181-200, pls. 11-12; Nilsson-Cantell, 1921, pp. 78-92, 98, 99, 100, 123-126, 129, text-figs. 13, 21; Kühnert, 1934, pp. 45-78, 24 figs.; Wells, 1966, p. 28 [not of Hancock, 1849] = *Kochlorine floridana* Wells and Tomlinson, 1966, *vide* Wells and Tomlinson, 1966, p. 28.

Trypetesa lampas (Hancock), Rathbun, 1905, pp. 79-80; Krüger, 1940, pp. 146, 147, 154, 155, 165, 273-279, 297, 328, 454, 473, figs. 151, 152, 154, 160, 161, 163, 167, 168, 265-270; Ross, 1965, p. 317; Boekschoten, 1966, p. 370, figs. 12-13; Turquier, 1967, pp. 75-78, fig. 1; Newman, Zullo, and Withers, 1969, p. R272; Tomlinson, 1969a, pp. 125-128, 150, fig. 34.

Trypetesa lampas is a burrowing cirriped, the burrows of which are found in a variety of gastropod and other shells. The female of the species only is the borer, and in the process of boring orients itself perpendicular to the surface of the host shell. *T. lampas* undergoes three stages of development — nauplius, metanauplius, and cyprid — and boring starts directly after metamorphism. At first the perforations are shallow oval pits; later these are enlarged to fan-shaped burrows with a slitlike aperture which is elongate, asymmetrically arcuate, and pointed at one end. The thickness of the species ranges from 1.72 to 4.12 mm, and a size of 11 mm in greatest diameter may be attained.

Type localities. — Off Whitburn, Durham (54°47'N, 1°21'W) and Cullercoates, Northumberland (55°02'N, 1°25'W), northeastern shores of England, 15 to 20 fathoms, imbedded in dead shells of *Fusus antiquus* Linnaeus and *Buccinum undatum* Linnaeus; southeastern shores of England, off the Eddystone Lighthouse.

Other localities. — England (Plymouth) on *Buccinum undatum*; North Sea, on *Fusus antiquus*; Sweden (west shore); West Germany (Island of Sylt; off Helgoland, 54°09'N, 7°52'E); Netherlands (Zoutkamp, Zuyder Zee, on *Buccinum undatum*, *Polynices catena* (da Costa), and *Neptunea antiqua* Linnaeus); Schiermonnikoog Island, (53°28'N, 6°10'E); France (Roscoff region, 48°43'N, 3°59'W), imbedded in *Buccinum undatum*, *Polinices catena*, *Littorina littorea* (Linnaeus), *Natica poliana* (Forbes), and *Turritella communis* (Risso); Mediterranean Sea; Western Atlantic, (along the east coast of the United States from the St. Lawrence to North Carolina). Massachusetts (Woods Hole, Falmouth, and Cape Cod, on *Lunatia heros* (Say) and *Polinices duplicatus* (Say); North Carolina.

It is not uncommon that shells infested with *Trypetesa lampas* are also occupied or have been occupied by hermit crabs of the genus *Pagurus*. However, all shells are not equally infested or occupied, as this depends on locality, season, size, and species of the host. An example of this was given by Turquier (1967, p. 77) who

listed the number of shells infested both with *T. lampas* and occupied by *Pagurus* in the Baie Morlaix, near Roscoff, France.

Host with <i>T. lampas</i>	Number occupied by <i>Pagurus</i>
<i>Buccinum undatum</i> Linnaeus	about 30 per hundred
<i>Natica catena</i> (da Costa)	22 per hundred
<i>Littorina littorea</i> (Linnaeus)	15 per hundred
<i>Natica poliana</i> (Forbes)	5 to 10 per hundred
<i>Turritella communis</i> (Risso)	3 to 4 per hundred

I have not seen *Trypetesa lampas* listed from Florida, the nearest locality to it being the coast of North Carolina, on *Lunatia heros*. However, *T. lampas* is also found in *Polinices duplicatus* and as that gastropod extends from Cape Cod to Florida and the Gulf of Mexico, the probability is that *T. lampas* will also be found eventually in Florida waters.

Order RHIZOCEPHALA F. Müller, 1862

Family **PELTOGASTRIDAE** Lilljebourg, 1861, p. 96

Briarosaccus callosus Boschma

Pl. 24, fig. 7

Peltogaster sp. Weltner, 1898, pp. 3, 4; Boschma, 1960, pp. 18, 19; Boschma, 1962, p. 58.

Briarosaccus sp. Boschma, 1960, pp. 18, 19; 1962, p. 58.

Briarosaccus callosus Boschma, 1930, pp. 1-8, figs. 1-8; 1960, pp. 18, 19; 1962, pp. 57-91, figs. 1-24, pl. I; 1970, pp. 233-236, 238, figs. 1b-e, 2; Krüger, 1940, pp. 168, 170, fig. 175h; Boschma and Haynes, 1969, pp. 97-98, fig. 1; Ross and Newman, 1969, pl. 17, maps 1, 4, fig.; McMullen and Yoshihara, 1970, pp. 818-821, fig. 1, table; Newman and Ross, 1971, pp. 10, 11, 23, 183, 185, fig. 90, Appendix 1.

The distinguishing external characters of the holotype of *Briarosaccus callosus* are its gigantic size (98 mm in antero-posterior diameter), its form in the shape of an inflated human kidney, and its attachment to the abdomen of the host at a right angle. At other localities or on different hosts, the body of *B. callosus* may vary from sausage-like and gently arcuate to tumid and "U" shaped. However, the internal anatomy, except perhaps for the structure of the male organs, is so much like that of the holotype, that Boschma, despite individual variation, dissimilar hosts, and a geographic range through extremes of polar and tropical waters, from the Bering Sea in the north to the Straits of Magellan in the South Atlantic, has tentatively united them under the same taxon.

Type locality. — "Albatross" sta. 2666 ($30^{\circ}47'N$, $79^{\circ}49'W$), east off Fernandina, Florida, attached to the anomuran crab *Lithodes agassizii* Smith, depth 270 fathoms. The syntype was trawled at "Albatross" sta. 2677 ($32^{\circ}39'N$, $76^{\circ}50'3''W$) off Cape Fear, North Carolina, in 478 fathoms.

Other localities. — Caribbean Sea: "J. E. Pillsbury" sta. 770 ($12^{\circ}55'N$, $71^{\circ}46.5'W$ and $13^{\circ}04'N$, $71^{\circ}42'W$), 36 statute miles north of Punta Gallina, Goajira Peninsula, Colombia. Attached to the abdomen of *Lithodes agassizii* at depths of 1,318 and 1,299 fathoms.

North Pacific: Bering Sea, "Albatross" sta. 3332 ($54^{\circ}02'50''N$, $166^{\circ}45'W$), south of Bering Island, 406 fathoms, host *Lithodes aequispinus* Benedict.

Gulf of Alaska, off Kodiak Island ($57^{\circ}58'N$, $153^{\circ}45'W$), host *Lithodes aequispinus*, 115 fathoms.

Alaska: Limestone Inlet ($58^{\circ}02'N$, $133^{\circ}59'W$), intertidal zone to 40 meters, and Auke Bay ($58.24^{\circ}N$, $134.40^{\circ}W$), on *Paralithodes camtschaticus* (Tilesius).

South Atlantic: "Discovery" sta. WS-764, east off Comodoro Rivadavia, Argentina from $44^{\circ}40'S$ and $62^{\circ}W$ to $44^{\circ}41'S$ and $61^{\circ}52'W$, depths 110 to 104 meters; from $45^{\circ}08'S$ and $60^{\circ}30'W$ to $45^{\circ}08'S$ and $60^{\circ}26.5'W$, on *Lithodes antarcticus* Jacquinot, depth 113-119 meters.

South Georgia Island: "Discovery" sta. 146 ($48^{\circ}S$, $35^{\circ}37'30''W$), depth 728 meters; "Discovery" sta. 158 ($48^{\circ}30'S$, $35^{\circ}57'W$), depths 401-411 meters, hosts *Lithodes antarcticus* Jacquinot and *Paralomis granulosa* (Hombron and Jacquinot).

Falkland Islands (west): $49^{\circ}54'S$, $60^{\circ}35'3''W$ to $51^{\circ}S$, $62^{\circ}02'30''W$, depths 64 to 207 meters; also "Discovery" stations WS-75, 76, 98, 225, 756, on *Paralomis granulosa* and *Lithodes antarcticus*.

Falkland Islands (east): "Discovery" sta. 56, Port William, on *Paralomis granulosa*, depths 10.5 to 16 meters.

Chile: Punta Arenas ($53^{\circ}10'S$, $70^{\circ}56'W$).

The known depth range of the hosts of *Briarosaccus callosus* is from the intertidal zone to 861 meters (470 fathoms). The shallowest occurrences are in the intertidal zone of Limestone Inlet, Alaska, and 10.5 meters in Sparrow Cove, Port William, in the East Falklands; the deepest is 861 meters off Cape Fear, North Carolina.

The hosts of the parasite *Briarosaccus callosus* are the crabs *Lithodes aequispinus* Benedict, in the Bering Sea; *Paralithodes camtschaticus* (Tilesius) in Alaskan and adjacent waters; *Lithodes agassizii* Smith, in the Western Atlantic off the northeast and southeast coast of the United States; *Lithodes antarcticus* Jacquinot, off Argentina, South Georgia Island, and the Falkland Islands; and *Paralomis granulosa* (Hombron and Jacquinot), off the Falkland Islands and South Georgia Island.

McMullen and Yoshihara (1970) demonstrated that infection by the parasites *Briarosaccus callosus* of the deep water crab *Lithodes aequispinus* is detrimental to the reproductive process of these crabs. In a sampling of 21 crabs captured near Kodiak Island, Alaska, the authors ascertained that 14 of them, or nearly 70 per cent, were infected by *B. callosus*. They also found that in the infected crabs the sex product maturation was greatly inhibited in mature female hosts either because they carried no eggs or no eggs were ripening in their ovaries. In healthy mature males, the testes are very evident, but in the infected males the testes were so impoverished as to be hardly visible. The king crabs in Alaskan waters are commercially important, and the finding by McMullen and Yoshihara of the high incidence of parasitism in the crabs, with the resulting adverse effect on reproduction, is a noteworthy contribution.

***Tortugaster fistulatus* Reinhard**

Pl. 25, figs. 7, 8

Tortugaster fistulatus Reinhard, 1948, pp. 33-37, figs. 1-3.

In shape, the parasite *Tortugaster fistulatus* resembles a mature *Peltogaster*, with the right side convex and the left side concave. The larger of the two specimens examined by Reinhard has the posterior side reflexed against the concave side. This posterior lobe is a region of the animal extending beyond the limits of the visceral mass and hence is softer and more susceptible to folding (Pl. 25, fig. 7A). The mantle opening, which is present at the anterior end of the mantle is relatively small, and is surrounded by a thick, elevated cushion formed by the sphincter. The stalk is approximately equidistant from the anterior and posterior ends but is peculiar in being shifted far to the left of the mid-dorsal line. The visceral mass is broadly attached to the mantle only in the region of the genital organs which lie to the right of the stalk. In the posterior third of the

animal the visceral mass is absent. The external cuticle is thin, measuring 5 to 8 microns; however, in the region of the stalk, the external cuticle increases in thickness, reaching a maximum of 30 microns in the wall of the stalk itself. There are no excrescences on the external cuticle but there are small indentations. The internal cuticle is thin and bears retinacula, consisting of one or two minute spindles having a height of 6 to 9 microns and a width of 2.3 to 3 microns. The testes are straight or slightly bent tubules. The larvae, which hatch in the cypris stage, are comparatively large and oblong, ranging from 150 to 200 microns in length and 70 to 100 microns in width. Two specimens of *T. fistulatus* were recovered, one each on the host crab *Munidopsis robusta* (A. Milne Edwards). The smaller of the two parasites, measuring 9 mm in length, 5 mm in width, and 3.5 to 4 mm in thickness, is here designated the paratype, and was collected July 31, 1930, by Dr. Waldo L. Schmitt. The larger parasite measured 10 mm $\times$ 6 mm $\times$ 4.5 mm and was collected August 5, 1932, also by Dr. Schmitt.

Type locality. — Off Tortugas, Florida, in 220 and 280 fathoms on *Munidopsis robusta* (A. Milne Edwards). The parasites were attached to the terminal segment of the crab's abdomen, on the ventral side, oriented with the mantle opening directed toward the right side of the host and with their long axis perpendicular to that of the host.

Peltogaster sp. H. W. Wells

Peltogaster species Wells, 1966, pp. 90, 91, 94.

According to Wells "this sacculinid parasite of hermit crabs has not been reported previously from the Gulf of Mexico." The parasite was discovered by Wells on the hermit crab *Pagurus longicarpus* Say from Live Oak Island, Wakulla County, Florida, and was collected first on November 3rd, 1962, and again on November 21st, 1963.

In certain regions, such as the vicinity of Beaufort, North Carolina, *Pagurus longicarpus* is a very common hermit crab and is particularly abundant in channels, "whence, by dredging, hundreds may be taken in a few hours" (Hay and Shore, 1918, p. 412). This suggests that eventually the rhizocephalid *Peltogaster* sp. Wells, which lives on the host *Pagurus longicarpus*, should also be found in abundance and will then be described formally.

Pagurus longicarpus has been identified from as far north as Minas Basin (45°15'N) in Nova Scotia; therefrom along the east coast of the United States to southern Florida; in the Gulf of Mexico off Florida and Texas; and in waters as far south as Brazil.

Family **SACCOLINIDAE** Lilljeborg, 1861, p. 96

Sacculina americana Reinhard

Pl. 21, fig. 1

Sacculina americana Reinhard, 1955, pp. 76-77, fig. 2.

The external sac is fig-shaped, broadest in the anterior half and tapering posteriorly to the stalk. The outline of the sac is relatively smooth to irregularly wavy. The surface is marked by minute sinuous striae with short side extensions, broken by widely spaced deeper grooves. The mantle opening is prominent, surrounded by a thick pad, and situated in the center of the anterior surface but turned to the left side. The stalk is short and in the same submedian plane as the mantle opening. The external cuticle has a ragged appearance. Of the four specimens of *S. americana* examined by Reinhard, the smallest, herein designated the type of the species, was 10 mm in length, 9 mm in breadth, and 4 mm in thickness; the largest was 15 mm × 13 mm × 5 mm.

Type locality.—The host, *Trachycarcinus spinulifer* Rathbun, collected at "Oregon" sta. 319 in the Gulf of Mexico at 29°20'N, 87°25'W, about 52 statute miles south-southwest of Pensacola, Florida. Four specimens of the parasite *S. americana* were found on one specimen of the host crab *Trachycarcinus spinulifer*, and these are in the USNM collection No. 96988. The cancrioid crab *T. spinulifer* was also reported by Rathbun (1930, p. 167) in the Gulf of Mexico south of the Florida-Alabama coast at the following stations:

"Albatross" sta. 2395 (28°36'15"N, 86°50'W), 347 f., gray mud, temp. 44.1°F.

"Albatross" sta. 2376 (29°03'15"N, 88°16'W), 324 f., gray mud, temp. 46.5°F.

Sacculina bicuspidata Boschma

Pl. 21, figs. 2, 3

Sacculina bicuspidata Boschma, 1931, pp. 312, 342-344, figs. 7L, 31, 32; 1937, pp. 212-213, fig. 8; Krüger, 1940, p. 167, fig. 174L; Reinhard, 1955, pp. 75-76, fig. 1.

The external sac of the holotype of *Sacculina bicuspidata* is broadly domal, with a flattened base and unevenly scalloped sides

which are subparallel below and slope in toward the mantle opening above. There is a deep median groove on the surface, this groove resulting from pressure of the host on the parasite. The mantle opening is elevated but not conspicuously so. The stalk is shorter than the mantle opening and in the same plane. The posterior angles of one adult specimen is drawn out into lappets. The external cuticle is marked with delicate rugae resembling fingerprints. In places the cuticle of the chitinous layer is almost smooth but in others there are minute excrescences of irregular shape; such differences, however, are gradual. The testes, which are located outside the visceral mass in the stalk region, are cylindrical, thick-walled, and separated into tubules of approximately equal size. The size of the parasite ranges from 3 to 6 mm in breadth, 3 to 5.5 mm in length, and 1.5 to 2.5 mm in thickness. The hosts to which *S. bicuspidata* has been found attached are the crabs *Microphrys bicornutus* (Latreille) and *Trachycarcinus spinulifer* Rathbun.

Type locality.—Tobago (British West Indies), 11°15'N, 60°40'W, on *Microphrys bicornutus*. Also reported from St. Thomas Harbor, Virgin Islands, 18°22'N, 64°57'W, on the same host, by Reinhard.

Florida locality—“Oregon” sta. 279, Gulf of Mexico, 29°11'N, 86°52'W, 305 fathoms, on *Trachycarcinus spinulifer*. “Oregon” sta. 279 is close to “Oregon” sta. 319, the type locality of *Sacculina americana* Boschma, which is about 52 statute miles south-southwest of Pensacola, Florida.

The spider crab *Microphrys bicornutus* (Latreille) is abundant and widespread in the Gulf of Mexico, the Western Atlantic, and the Caribbean Sea. It has been reported from Bermuda, off the coasts of North Carolina and South Carolina, in many localities around Florida and the Bahama Islands, off Cuba, Jamaica, Puerto Rico, St. Thomas, St. Eustatius, Barbados, Tobago, Trinidad, Curaçao, Colombia, Panama, and Brazil. Depths range from 0.25 fathoms (Curaçao) to 37 fathoms in the Straits of Florida (Rathbun, 1925, pp. 489-495).

***Sacculina boschmai* Reinhard**

Pl. 22, fig. 3

Peltogaster sp. Rathbun, 1937, p. 227.

Sacculina boschmai Reinhard, 1955, pp. 77-79, figs. 3-4.

The parasite is rounded tetragonal, the sac one-third broader

than long, convex at the anterior and posterior margins, and strongly arched at the dorsal and ventral margins. The stalk is prominent, arising from a depression on the left side of the body near the posterior end. The mantle opening is small, subcircular, shifted slightly to the left, and occupies the center of the anterior surface opposite the stalk. The mantle opening is encircled by a heavy ridge bearing prominent folds radiating away from the apex. At the exit from the mantle cavity the body wall increases more than three times in thickness where it forms the thick folds around the mantle opening. In surface view the external cuticle has a rough shark-skin appearance due to the numerous closely spaced excrescences. The type specimen (USNM 96989) is 12 mm in maximum diameter, 9 mm in width, and 5 mm in thickness.

Type locality. — "Albatross" sta. 2401, Gulf of Mexico, 28°38' 30"N, 85°53'30"W, depth 142 fathoms, collected March 14, 1885. One specimen of *S. boschmai* was found on the host *Acanthocarpus alexandri* Stimpson from a bottom of green mud and broken shells. The type locality is about 180 statute miles south-southeast of Pensacola, Florida, and 265 statute miles west of Tampa, Florida.

According to Reinhard, the male *Peltogaster* sp. of Rathbun, attached to the oxystomatous crab *Acanthocarpus alexandri*, is identifiable as *Sacculina boschmai*.

Acanthocarpus alexandri is widespread in the Western Atlantic, Gulf of Mexico, and the Caribbean Sea. From north to south it occurs off Massachusetts, North Carolina, South Carolina, east and west coasts of Florida, Puerto Rico, Saba Bank, St. Kitts, and the Grenadines (Rathbun, 1932, pp. 226-227). At the localities mentioned, depths range from 45 fathoms (Tortugas, Florida) to 208 fathoms off St. Kitts on bottoms generally of mud and rarely of sand, shells, corals, or ooze. The temperatures of the bottom water range as low as 49°F. off Martha's Vineyard to 76°F. off St. Kitts. This distribution of the host crab suggests that its parasite *Sacculina boschmai* will also be found to be widespread.

***Sacculina hirsuta* Boschma**

Pl. 22, figs. 4-6

Sacculina hirsuta Boschma, 1925, pp. 10-11, text-fig. 1, pl. 2, figs. 1, 5; 1931, pp. 311, 312, 339-342, figs. 7j, 30; 1937, pp. 260-261, fig. 45; Reinhard, 1950a, p. 127.

The holotype of *Sacculina hirsuta* is oval in shape and com-

pressed laterally, with its thickness almost half the breadth. At the type locality — Caracasbaai — the entire surface of the parasite is provided with grooves (Pl. 22, fig. 4), the grooves deeper in the marginal parts of the sac and shallower in the central part of each lateral surface. However, on a specimen from St. Thomas in the Virgin Islands, the surface is comparatively smooth except for a few furrows at the anterior margin (Boschma, 1931, fig. 7j). The mantle opening is situated at the top of a small papilla which itself is grooved. The papilla occurs on the surface which is directed toward the thorax of the host crab, near the free edge. The surface of the parasite which was pressed against the abdomen of the crab is deeply hollowed out. The external cuticle is covered with hairlike excrescences which are 35 microns in length near the mantle opening but much shorter in the region of the stalk. Each excrescence has a blunt, more or less rounded extremity which is often enlarged to claviform proportion. The excrescences arising from the cuticle of the St. Thomas specimen consist of smooth hairs, stiffer than those from Caracasbaai, Curaçao, and lacking the numerous small lateral hairs of the Curaçao form. As pointed out by Boschma in a later description of *Sacculina hirsuta* (1937, p. 260) the left testis is larger than the right. The type specimen measures 5 mm in breadth, 3.5 mm in height, and 2.5 mm in thickness.

Type locality. — The type locality of *Sacculina hirsuta* is Caracasbaai, Curaçao, in the Netherlands Antilles. The host crab to which *S. hirsuta* was attached is *Pilumnus caribaeus* Desbonne and Schramm.

Other localities. — St. Thomas (18°22'N, 65°57'W), Virgin Islands, on the host *Pilumnus dasypodus* Kingsley, and at Black Rock, off the Neuse River, North Carolina, also on the crab *Pilumnus dasypodus*. I have seen no report of *S. hirsuta* from Florida waters, but because the parasite has been found north and south of Florida, and because the host crab *Pilumnus caribaeus* ranges from the Florida Keys to Brazil and the other host crab *Pilumnus dasypodus* from North Carolina to Brazil, the discovery of *S. hirsuta* off Florida proper is just a matter of time.

***Sacculina pustulata* Boschma**

Pl. 22, figs. 7-10

Sacculina pustulata Boschma, 1925, pp. 11-12, text-figs. 2, 3, pl. 2, figs. 2, 6, 7; 1937, pp. 298-299, fig. 73; Reinhard, 1955, p. 79, fig. 5D; H. W. Wells, 1966, pp. 90, 92.

Even when fully mature this parasite is small, its greatest diameter ranging from 2 to 3 mm, its height from 2 to 2-1/2 mm, and its thickness from 1 to slightly less than 2 mm. The external sac, which is attached to the abdomen of the host by a short stalk, is nearly circular and laterally compressed in form. The mantle opening is situated at the extreme anterior margin of the sac lying on the top of a small papilla on either side of which is an indentation in the margin of the animal. Similar indentations are present next to the stalk, so that the posterior margin projects with an earlike protrusion at each side of the stalk. There is a shallow groove on that surface of the parasite which was pressed against the abdomen of the host. Externally, the mantle of *S. pustulata* is minutely pustulate, the pustulations caused by the pressure of the eggs in the mantle cavity which are visible by virtue of the transparency of the external cuticle. The mantle is covered by an external cuticle 8 to 12 microns in thickness, made up of chitin and parallel with the mantle. The upper surface of the external cuticle is divided into small knobs of approximately the same size, their transverse diameter varying from 12 to 16 microns. These knobs are separated by small shallow grooves (see Pl. 22, figs. 9, 10) presenting a neat hexagonal pattern. The testes are completely separated, unequal in size, and located outside the visceral mass. The type specimen of *S. pustulata* measured 3 mm in greatest breadth, 2-1/2 mm in height, and slightly less than 2 mm in greatest thickness in the central part of the body. This is about half the size of the host which itself is the small spider crab *Hemus cristulipes* A. Milne Edwards.

Type locality. — Spaanse Water, Curaçao, Netherlands Antilles. One example on *Hemus cristulipes*, female.

The only other locality I have seen reported for the rhizocephalid parasite *Sacculina pustulata* is in the Gulf of Mexico, 10 miles southeast of Alligator Point, Franklin County, Florida, depth of 6 fathoms, where it is parasitic on the same spider crab — *Hemus cristulipes* — as in Curaçao. *Hemus cristulipes* ranges from northern Gulf of Mexico to at least as far south as Curaçao, living in shallow water up to 27 fathoms according to Rathbun (1925, pp. 345-347, text-fig. 110, pl. 124, fig. 1; pl. 248, figs. 9-15).

***Sacculina rathbunae* Boschma**

Pl. 23, figs. 4-6

Sacculina rathbuni Boschma, 1933, pp. 222-223, fig. 4; 1937, pp. 299-300, fig. 74; Krüger, 1940, pp. 196-198, fig. 208-1.

Sacculina rathbunae Boschma, 1950, pp. 4, 9-10, fig. 1d; Reinhard, 1955, p. 80, fig. 5E.

The external sac of the holotype *Sacculina rathbunae* is smooth, rounded hexagonal in form, inflated circularly over most of the body but appressed around the margin, and flattish anteriorly and posteriorly. There is an asymmetric indentation on each side of the mantle opening, and a deeper oblique indentation next to the dorsal side of the stalk. The mantle opening lies at the top of a small, short, erect tube at the anterior margin, and is situated at about the mid-line opposite the stalk. The stalk is broader than the mantle opening, slightly produced, and flared at the extremity. The dorsal and ventral ends of the margin are extended to form nipple-like prominences. The external surface of the cuticle is smooth and very thin (3 to 6 microns). The male genital organs are within the visceral mass. The testes are tubular, completely separated, and have approximately the same size and shape. The reticula is not known. The type specimen is 4.5 mm in breadth, 3 mm in height, and 1.5 mm in greatest thickness.

Type locality.—The type of the parasite *Sacculina rathbunae* was attached to a male crab, *Arachnopsis filipes* Stimpson, collected March 1, 1889 in the Gulf of Mexico at "Grampus" sta. 5076 (25°34'N, 83°28'W), depth 39 fathoms, bottom of gravel, coral, and fine shells. This location is 155 statute miles west of Highland Point on the southwest coast of Florida.

Other localities.—Los Roques Islands, Venezuela, on the arrow-crab *Stenorhynchus seticornis* (Herbst); off Barbados, depth 80 fathoms, on *Arachnopsis filipes*, collected by the "Hassler" December 1871.

For further information on the crab hosts *Stenorhynchus seticornis* and *Arachnopsis filipes* see Rathbun, 1925, pp. 13, and 89, respectively.

***Sacculina reniformis* Boschma**

Pl. 23, figs. 7-9

Sacculina reniformis Boschma, 1933, p. 227, fig. 9; 1937, pp. 300-301, fig. 75; 1950, pp. 4, 19, figs. 1i, 6b; Reinhard, 1955, p. 77, figs. 5A-C.

The external sac is kidney-shaped, the anterior surface and sides rounded, the posterior rendered lobular by the indentations on each side of the stalk. The stalk is short, slightly flared at the attachment end, and lies opposite the mantle opening. The mantle opening of

Boschma's type lies at the extremity of a short, wide tube in the center of the anterior region. On Reinhard's specimens the mantle opening is small and inconspicuous, and protrudes but little on the surface. The external cuticle is covered with small dentate excrescences which have a smooth surface and vary in height between 3 and 9 microns. There are a few short hairs on the tops and sides of these processes but none was observed on the type. Reinhard also found retinacula on the internal cuticle of his examples which were dispersed into single spindles, extremely variable in size and shape, ranging from 14 to 35 microns in length. The male genital organs are situated in the posterior part of the body outside the visceral mass. The testes are of about equal size, united in their dorsal part. The type of *Sacculina reniformis* measured 4.5 mm in breadth, 3 mm in height, and about 1.5 mm in thickness. The largest specimen examined by Reinhard was 7 mm in breadth, 4.5 mm in height, and 4 mm thick. The hosts of *S. reniformis* are the spider crabs *Podochela riisei* Stimpson and *Collodes leptocheles* Rathbun. The parasite *S. reniformis* has been reported only from the Gulf of Mexico off Florida, although the range of *Podochela riisei* is from North Carolina to Brazil, in shallow water to 30 fathoms, and the range of *Collodes leptocheles* from northern Gulf of Mexico to Puerto Rico, 69 to 169 fathoms.

Type locality. — The type locality of *Sacculina reniformis* is "Fish Hawk" sta. 7351 (25°09'0.45"N, 81°18'35"W), near Cape Sable, Florida. The host was *Podochela riisei*, collected December 16, 1912 in 3.25 fathoms, on a rocky coral bottom.

Other Florida localities. — Boschma — "Fish Hawk" sta. 2716 (28°26'30"N, 83°08'W), about 9 statute miles southeast of Cedar Key, Florida. On *Podochela riisei*, 10 fathoms, sandy and grassy bottom, temperature 13.6°F. "Fish Hawk" sta. 7147 (29°52'10"N, 83°51'47"W), about 14 statute miles south of the Aucilla River. On *Podochela riisei*, 3 fathoms, sand and coral bottom, temperature 20°F. Reinhard — "Oregon" sta. 36 (28°30'N, 85°36'W), about 55 statute miles south of Cape San Blas, Florida. On *Callodes leptocheles*, 120 fathoms.

***Sacculina schmitti* Boschma**

Pl. 22, figs. 1, 2

Sacculina schmitti Boschma, 1933, p. 229, fig. 11; 1937, pp. 305-306, fig. 79; 1950, pp. 20-21, figs. 1k, 12a.

The holotype of the parasite is broadly heart-shaped, with the lateral posterior parts of the sac extending beyond the stalk (Pl. 22, fig. 1). The body is slightly inflated and relatively even-surfaced but with some grooves and depressions. The external cuticle of the mantle is smooth, varying in thickness from 4 to 16 microns. The mantle opening lies at the extremity of a small tube in the central part of the anterior region. The stalk, which is prominent, is recessed between the projecting lobes of the sac. The male genital organs are in the posterior part of the body, outside the visceral mass. The testes are subglobular, nearly completely united save at the extreme dorsal parts. Retinacula were found. The type of *Sacculina schmitti* measured 5 mm in breadth, 5 mm in height, and about 1 mm in thickness. It was found attached to the spider crab *Anomalothir furcillatus* (Stimpson).

Type locality.—The crab *Anomalothir furcillatus* was collected in the Gulf of Mexico at "Albatross" sta. 2401 (28°38'30"N, 85°52'30"W), about 77 statute miles southwest of Cape San Blas, Florida, at a depth of 142 fathoms, on a bottom of green mud and broken shells.

Although the rhizocephalid *Sacculina schmitti* has been reported only from "Albatross" sta. 2401, it is likely to be found elsewhere in the Gulf of Mexico, the Western Atlantic, and the Caribbean Sea as the host *Anomalothir furcillatus* ranges from North Carolina to Grenada (11°48'15"N, 61°48'45"W), where it has been found at depths from 30 to 262 fathoms (see Rathbun, 1925, p. 26).

***Sacculina tessellata* Boschma**

Pl. 23, figs. 1-3

Sacculina tessellata Boschma, 1925, pp. 12-13, text-figs. 4-5, pl. 2, figs. 3, 8-10; 1937, p. 320 [= *Heterosaccus tessellatus* (Boschma), *vide* Boschma.]

The parasite *Sacculina tessellata* is heart-shaped, with the subtruncate posterior margin having the greatest breadth and with the anterior margin obtusely attenuated. One side of the body, along the mantle opening — stalk axis, is traversed by a longitudinal ridge directed toward the thorax of the host crab; the other side of the body is traversed from the mantle opening to the stalk by a deep furrow produced by pressure against the abdomen of the host. The mantle opening, which is wide, lies at the top of a small papilla at the anterior pole, somewhat nearer to the thorax than to the abdomen of the host. The external surface of the mantle consists of wartlike pro-

trusions bearing short excrescences 6 to 12 microns in height. The protrusions are separated by fine grooves which divide the external surface into a neatly tessellate pattern. The external surface consists of two parts, the upper one tessellated, the lower consisting of parallel layers of chitin with a uniform thickness of 12 to 16 microns. The male genital organs are composed of two well-developed testes, approximately the same in size and length, the left testis situated anterior to the right one. The type specimen of *S. tessellata* measured 4-1/4 mm in breadth, 4 mm in height, and 1-1/4 mm in thickness.

Type locality. — Caracasbaai, Curaçao, Netherlands Antilles, on *Mithrax* (*Mithraculus*) *ruber* (Stimpson). According to Rathbun (1925, pp. 432-433; 1933, p. 32), the spider crab *M. ruber* ranges from northwest Cuba (Cabañas Bay) to Curaçao, via Puerto Rico, St. Thomas, Water Island, Antigua, Guadeloupe, and Barbados, in shallow water to 84 fathoms (off Needham Point, Barbados). Cabañas Bay, Cuba, lies about 140 statute miles southwest of Key West, Florida.

***Heterosaccus occidentalis* (Boschma)**

Pl. 24, figs. 5,6

Depranorchis occidentalis Boschma, 1928, pp. 4-6, figs. 1a-d, 2, 3a-h.

Heterosaccus occidentalis (Boschma), 1931, pp. 359-361, fig. 43a, b; 1933, p. 231.

The body of *Heterosaccus occidentalis* is moderately and selectively inflated. In form it varies from subpentagonal with subrounded extremities to rounded subtrigonal. There is a medial surface depression of varying width along the axis of the mantle opening to the stalk. The mantle-opening is in the upper part of the sac, and is suboval and wide; the stalk is in the lower part of the sac, and lies approximately opposite the mantle opening. The size of the body varies from 4 mm or less to 11.5 mm as measured from the dorsal to the ventral surface, or at right angles with the axis through the mantle opening and stalk.

Type locality. — Deadman's Bay, off Steinhatchee, west coast of Florida — No. 60608 USNM, "Fish Hawk" sta. 7153, on *Mithrax forceps* (A. Milne Edwards).

Other localities. — Off Florida on *Macrocoeloma camptocerum* (Stimpson); on *Microphrys bicornutus* (Latreille); on *Pitho anisodon* (von Martens); on *Pitho lherminieri* Schramm at Key West

and off west coast; and on *Stenocionops furcata* (A. Milne Edwards). Bahama Islands on *Microphrys bicornutus* (Latreille); and on *Mithrax* (*Mithraculus*) *forceps* (A. Milne Edwards). Cuba on *Macrocoeloma diplacanthum* (Stimpson); and on *Microphrys bicornutus* (Latreille). Jamaica on *Mithrax* (*Mithraculus*) *sculptus* (Lamarck). St. Croix (Christiansted).

The distribution of the parasite *Heterosaccus occidentalis* and the hosts on which the species sustains itself, as given above, is from Boschma (1928, p. 6). The distribution of the host crabs as given by Rathbun (1925) and by Abele (1970) is as follows:

Mithrax (*Mithraculus*) *forceps* (A. Milne Edwards) ranges from off North Carolina and Bermuda, southward via the Gulf of Mexico, the Caribbean Sea, and the Western Atlantic to Brazil, in depths of one foot to 30 fathoms, generally on rocky, shelly or sandy bottoms.

Mithrax (*Mithraculus*) *sculptus* (Lamarck) ranges from Florida and the Bahamas to the Arquipélago dos Abrolhos, Brazil, via British Honduras, Swan Islands, Isla de Providencia (Colombia), Cuba, Jamaica, Puerto Rico, St. Thomas, Antigua, Barbados, and the Netherlands Antilles, in depths of 0.5 to 30 fathoms.

Macrocoeloma camptocerum (Stimpson) is reported from the waters off North Carolina and around Florida at depths of 2 to 19 fathoms, on sand-*Thalassia*, rocky, and coral or shelly bottoms.

Macrocoeloma diplacanthum (Stimpson) is a shallow-water crab (3 to 13 fathoms), occurring in Florida and the Bahamas, Jamaica, Puerto Rico, St. Croix, St. Thomas, Guadeloupe, Isla de Providencia, and Curaçao in the Netherlands Antilles.

Pitho anisodon (von Martens) ranges from Florida to Curaçao, via the Bahamas, Cuba, Jamaica, Puerto Rico, and Guadeloupe. Depths range from 2 feet to 12 fathoms, and the bottoms may be grassy, sandy, muddy, or rocky and coral-strewn. The few bottom temperatures recorded range from 15°C to 21°C.

Pitho lherminieri Schramm is known from near Beaufort, North Carolina, to Brazil, via South Carolina, Florida, the Bahamas, Mexico, Cuba, Jamaica, Puerto Rico, St. Thomas, St. Croix, Guadeloupe, Martinique, Isla de Providencia, and Curaçao, in 1-120 fathoms, on rocky, sandy, or coralline bottoms.

Stenocionops furcata (A. Milne Edwards) is reported from

Georgia (Savannah), Florida, Jamaica, Puerto Rico, St. Thomas, Dominica Island, and Barbados, in shallow water to depths of 35 fathoms, on coralline, shelly, or sandy bottoms.

Microphrys bicornutus (Latreille) ranges from Beaufort, North Carolina to Brazil, where it occurs at a number of localities. Intermediate stations are Bermuda, Florida (numerous localities), the Bahama Islands, Cuba, Jamaica, Puerto Rico, St. Thomas, St. Eustatius, Barbados, Panama, Isla de Providencia, Colombia, Curaçao, and Trinidad. Recorded depths are 1 foot to 15 fathoms, and the bottoms are rocky or coralline. Around Montego Bay, Jamaica, *Microphrys bicornutus* has been found among mangrove roots.

***Loxothylacus bicorniger* Boschma**

Pl. 26, figs. 6, 7

Loxothylacus bicorniger Boschma, 1933, pp. 240-241, figs. 22a-d; 1940, p. 279; 1950, pp. 5, 53-55, figs. 2L, 35; 1968, pp. 21, 24, 25, 26.

The sac of the parasite *Loxothylacus bicorniger* (see Pl. 26, fig. 6) is pentagonal in shape, with the dorsal and ventral extremities elongated into subangular prominences. On the right side there is a broad concavity in the vicinity of the stalk, caused by the pressure of the abdomen of the host against the parasite. The stalk itself is short, and the base of the sac is more or less flattish. The broadly ovate mantle opening is situated in the central part of the anterior region and lies at the end of a short tube with a well-developed wall. Within, the male organs are found in the posterior region of the visceral mass where the left testis is much larger than the right. The type specimen of *L. bicorniger* measured 8 mm in breadth, 5 mm in height, and 2.5 mm in thickness.

Type locality.—Hog Island, off Nassau, New Providence Island, Bahamas. The host was *Portunus ventralis* (A. Milne Edwards), to which were adherent two specimens of the parasite *Loxothylacus bicorniger*; the larger of these was designated the type by Boschma.

Hog Island lies about 200 statute miles due east of Key Largo, Florida. The host crab *P. ventralis* ranges from off Georgia and north Florida to the Tortugas of Florida, through the waters of Cuba, Jamaica, Puerto Rico, St. Thomas and Barbados, to as far south as Cabo Frio, Brazil. It seems likely that the parasite *Loxothylacus bicorniger* will also be found in the same waters.

***Loxothylacus engeli* Boschma**

Pl. 26, figs. 4, 5

Loxothylacus engeli Boschma, 1968, pp. 21-26, figs. 1-4.

The parasite is rounded or slightly oval, its thickness about half the greatest diameter. The mantle opening lies at the top of a plump roundish papilla containing the well-developed sphincter. The stalk lies opposite the mantle opening and is attached, at some distance from the visceral mass, to a shallow concavity of the mantle in the middle of the posterior surface. With the exception of a broad surface furrow in the middle of the right side, resulting from pressure of the median ridge of the host's abdomen against the parasite, the mantle is smooth, without grooves or conspicuous wrinkles. The external cuticle of the mantle also has a smooth surface, lacking excrescences. The internal cuticle of the mantle bears retinacula, each of which has about 8 barbed spindles with a length of 16 microns. The two male organs are of approximately equal size and structure with but little curvature. The type measures 7 mm in dorso-ventral diameter, 6 mm in antero-posterior diameter, and 3.5 mm in thickness. The host is the spider crab *Anasimus latus* Rathbun which ranges from the northern Gulf of Mexico and the Western Atlantic off the coast of South Carolina (32°54'N, 77°3'30"W) to Florida and the Caribbean Sea at 10°37'N, 61°42'40"W, between Venezuela and Trinidad.

Type locality. — "Coquette" sta. 32, 6°51'N, 54°53.5'W, depth 28 fathoms, bottom of mud and shells. Collected 12 May 1957, northeast of the mouth of the Suriname River. One specimen, on *Anasimus latus* Rathbun.

I have seen no report of *Loxothylacus engeli* in Florida waters, but inasmuch as the host *Anasimus latus* has been found in a number of places around Florida, it is anticipated the parasite will also be found.

***Loxothylacus longipilus* (Boschma)**

Pl. 26, figs. 1-3

Sacculina longipila Boschma, 1933, pp. 220-221, figs. 2a-c; Krüger, 1940, pp. 170, 178, fig. 187d.

Loxothylacus longipilus (Boschma), Boschma, 1950, pp. 4, 7-8, figs. 1b, 5a-e.

The sac of this species is inflated and subhemispherical in outline, with a pronounced concavity at the base on the right side near the stalk (see Pl. 26, fig. 1). The mantle opening, which lies at the

anterior margin of the left side, somewhat eccentrically, is suboval and thickened around the aperture. The mantle does not possess any pits or grooves, and the visceral mass is attached to it some distance from the stalk. The male genital organs are in the visceral mass, and the right testis, which shows a distinct curve, is larger than the left. The type measures 2.75 mm in breadth, 2 mm in height, and 1.5 mm in thickness.

Type locality. — Barbados, British West Indies, attached to the host crab *Micropanope lobifrons* A. Milne Edwards. The type specimen is in the U.S. National Museum (National Museum of Natural History). It was collected by the Barbados-Antigua Expedition June 5, 1918.

In Florida waters the cancrioid crab *Micropanope lobifrons* has been reported by Rathbun (1930) in the Gulf of Mexico south of St. George Island at 28°46'N, 84°49'W, at a depth of 26 fathoms, on a coarse sand and coral bottom; in the Tortugas; and 2.5 miles south-southeast of Fowey Rocks Light (25°35'N, 80°05'W), in the Straits of Florida, southeast of Miami, at a depth of 45 feet, on a rocky bottom. It is anticipated, therefore, that the parasite *Loxothylacus longipilus*, will also be found in Florida.

Additional localities of *Micropanope lobifrons* are off Habana, Cuba; the Virgin Islands, 20-23 fathoms; Barbados, at six stations, mostly rocky bottoms, depths 20-75 fathoms; Grenada, 170 fathoms; and Panama, near Colon at 9°32'N, 79°54'30"W, 34 fathoms, bottom of gray ooze and broken shells.

***Loxothylacus panopaei* (Gissler)**

Pl. 26. figs. 8-15

Sacculina panopaci Gissler, 1884, pp. 225-229, figs. 1-2; Weltner, 1897b, p. 234; Smith, 1906, p. 113; Boschma, 1928a, p. 172; 1937, p. 287.

Loxothylacus panopaei (Gissler), Boschma, 1928a, p. 172; 1928b, pp. 6-10, figs. 4a-d, 5, 6; 1931, pp. 365-368, figs. 33i, j, 48; 1933b, p. 231; 1937, p. 287; 1940, p. 277; 1950, p. 7; Reinhard and Reischman, 1958, pl. I; H. W. Wells, 1966, pp. 90, 92, 93.

Loxothylacus panopaei (Gissler), Behre, 1950, p. 17; Reinhard, 1954, pp. 67-71, figs. 1-5.

Gissler's type species of this rhizocephalid was a female 2-7/8 mm in thickness, 6 mm in width and 4-3/5 mm in length, and was attached to the "third segment on the ventral surface of the abdomen" of a female crab, *Panopeus herbstii* A. Milne Edwards.

As later described by Boschma and Reinhard, the external out-

line of the body varies from smoothish to wrinkled. The spines of the external cuticle are relatively long. In some specimens the mantle opening lies at the top of a small tubelike expansion of the mantle, but in others the mantle opening is surrounded by a muscular mass which does not project above its vicinity. The stalk is short and flared slightly at its posterior extremity.

Type locality. — Tampa Bay, Hillsborough County, Florida; on *Panopeus herbstii*.

Other Florida localities. — Key West, on *Panopeus herbstii*; Inglewood (26.58°N, 82.21°W), on *Panopeus herbstii*; 15 miles south of Alligator Harbor, depth 60 ft., on the hairy crab *Pilumnus sayi* Rathbun; St. Andrews Bay, on the mud crab *Neopanope packardii*; south of Pensacola at "Oregon" sta. 36 (28°30'N, 85°36'W), on *Tetraxanthus rathbunae* Chase, depth 120 fathoms.

Distribution. — *Loxothylacus panopaei* is parasitic on hosts reported in the Americas from as far north as Alaska in the Eastern Pacific to as far south as southern Brazil in the Western Atlantic. Excepting those in Florida, given above, the occurrences of *Loxothylacus panopaei* are the following: Louisiana (Grand Isle, on *Panopeus herbstii*; Barataria Bay, on *Rhithropanopeus harrisi* (Gould); Bay St. Elaine, on *Panopeus herbstii*; Bassa Bassa Bay and Bay Chêne Fleur, on *Eurypanopeus depressus* (Smith). Texas (head of Copano Bay), on *Eurypanopeus depressus* and *Rithropanopeus harrisi*. Cuba, on *Panopeus herbstii*. Jamaica, on *Panopeus herbstii*. Puerto Rico, on *Panopeus occidentalis* (Saussure). St. Croix (Christiansted Lagoon), on *Panopeus occidentalis*, (depth 0.5 m). Venezuela (off Puerto Cabello, on *Tetraplax quadridentata* (Rathbun). Brazil. Canada (Dodds Narrows, Nanaimo, British Columbia), on *Lophopanopeus bellus* (Stimpson).

***Loxothylacus perarmatus* Reinhard and Reischman**

Pl. 27, figs.1-9

Loxothylacus perarmatus Reinhard and Reischman, 1958, pp. 95-97, pl. 2.

Loxothylacus perarmatus is a plump reniform parasite with a chitinous external cuticle possessing numerous minute excrescences, furrows, and pits. The mantle opening is thickened and elevated and is displaced slightly to the left side. The stalk, which measures 2.3 mm in diameter, is short, heavily chitinized, and flared at the ex-

tremity. The type specimen is 12 mm in length, 18 mm in thickness, and 8 mm in breadth.

Type locality. — "Oregon" sta. 218 (22°27'N, 89°34'W), Gulf of Mexico, about 85 statute miles north of Progreso, Yucatan (Mexico), and 475 miles west-southwest of Key West, Florida. The type species was attached to the spider crab host *Parthenope (Platylambrus) pourtalesii* (Stimpson) which was recovered January 10, 1951, at a depth of 124 fathoms.

The host crab *P. pourtalesii* ranges from Martha's Vineyard, Massachusetts, to Habana, Cuba, in waters ranging from 10 to 134 fathoms in depth, via New Jersey, North Carolina, South Carolina, and Florida. Florida localities are off Fowey Rocks, Ragged Key, Sambo Key, Sand Key, Key West, and on the submerged Pourtales Plateau. Because the continental shelf along the west coast of Florida is similar to that off Yucatan, and because the host crab *Parthenope pourtalesii* occurs abundantly in Florida waters, there is little doubt that the parasite *Loxothylacus perarmatus*, which is attached to that crab, will also be found abundantly around Florida.

***Loxothylacus texanus* Boschma**

Pl. 27, figs. 10-14

Loxothylacus texanus Boschma, 1933, p. 237, fig. 20; 1940, p. 278; 1950, pp. 43-50, figs. 2i, j; 3b, c, e; 27-31; Reinhard, 1950b, pp. 360-365, figs. 1-4; Hopkins, 1957, p. 426.

Loxocephalus texanus (Boschma), Pearse, 1952, p. 238; 1952a, p. 7; Menzel, 1956, p. 40; Wells, H. R., 1966, pp. 90, 93.

This species is one of the largest known representatives of the genus *Loxothylacus*.

The shape of the parasite, although generally reniform, is variable (see Pl. 27, figs. 10-12). The external sac may be broadly oval and bilobular, or irregularly oval, or even orbicular, and the surface may be smoothish or irregularly wrinkled or scalloped. Viewed from the right side, most specimens exhibit a longitudinal furrow running from the stalk to the mantle opening. This furrow "is caused by the median ridge of the crab's abdomen which presses against the right side of the parasite. The left side which faces the thorax of the host, usually has a slight longitudinal elevation which is caused by pressure against the grooved sternal plastron of the crab." (Reinhard, 1950, p. 361).

The mantle opening is directly opposite the stalk but appears to

be displaced slightly to the left. The mantle opening is thickened, usually somewhat elevated, and marked by grooves and ridges. The stalk, which attains a diameter of 5 mm in fully grown examples, is short, slanting, and a little chitinized.

The external cuticle bears short but unequal and randomly spaced excrescences.

Measurements of the body of *L. texanus*, as given by Boschma and by Reinhard, vary from 8 mm to 24 mm in dorso-ventral diameter, 5 mm to 17 mm along the antero-posterior axis (height), and 3 mm to 8 mm in thickness. The average is 16 mm $\times$ 8.2 mm $\times$ 5 mm.

The hosts of *Loxothylacus texanus* are the crabs *Callinectes sapidus* Rathbun and *Callinectes marginatus* (A. Milne Edwards).

Type locality.—Matagorda Bay, near Indianola, Texas. In Texas the species also occurs in San Antonio Bay, and in estuaries a few miles eastward of Port Aransas (27.50°N, 97.05°W), all of them on the blue crab *Callinectes sapidus*.

Florida localities.—St. George Sound and Alligator Harbor, Franklin County, on *Callinectes sapidus*.

Distribution.—The parasite *Loxothylacus texanus* has been reported from Texas to Florida in the Gulf of Mexico on the edible blue crab *Callinectes sapidus*, and from the Republic of Panama in the Bello River and Panama Canal Zone, including Toro Point, on *Callinectes marginatus*.

As stated by Rathbun (1930, pp. 106-111; pp. 124-127), the hosts *Callinectes sapidus* and *Callinectes marginatus* are widely distributed species. *Callinectes sapidus* ranges from Nova Scotia to Uruguay in the Western Atlantic, from Texas to Florida in the Gulf of Mexico, and from Cuba to Nicaragua and Panama in the Caribbean. *Callinectes marginatus* extends from Bermuda, Florida, and the Bahamas to Ilha São Sebastião, Brazil, in the Western Atlantic; from Mexico, Louisiana, and Florida in the Gulf of Mexico; from Cuba through the Antilles to Venezuela in the Caribbean; and from the Cape Verde Islands to and along the west coast of Africa in the Eastern Atlantic.

I have been unable to find the original reference to "*Loxocephalus*" *texanus* Boschma referred to in the synonymy of this paper. However, I believe it must be the same species as *Loxothylacus*

texanus Boschma since both taxa are reported from the Gulf of Mexico where they are parasitic on the same host *Callinectes sapidus*.

Callinectes sapidus has been found as a fossil on Gaugatha Beach, Accomac County, Virginia, where, according to Rathbun (1895, p. 354), it may have been transported from extensive Miocene beds exposed along that coast. *C. sapidus* also occurs in the Talbot Formation of Pleistocene age at Cook Point, Dorchester County, Maryland (Clark, 1906, p. 174, pl. XLI). It is postulated that *Callinectes sapidus* was infested with rhizocephalan parasites during late Cenozoic and Pleistocene times, but whether the parasites were the same species as today's *Loxothylacus texanus* will be difficult to ascertain even in the remote likelihood of their being adequately preserved.

***Ptychascus glaber* Boschma**

Pl. 24, figs. 1-4

Ptychascus glaber Boschma, 1933a, pp. 532-537, figs. 43-48; 1967, pp. 321-323, figs. 1-2; Krüger, 1940, pp. 168, 294, 296, fig. 175i.

This parasite is characterized by its long narrow tube, at the extremity of which is the mantle opening. The tube, which attains a length of 2 mm, is directed toward the dorsal surface of the animal, and is straight or somewhat curved (Pl. 24, figs. 1, 4). The external sac is bilaterally subsymmetrical, more or less oval in shape, variously subangular, rounded, or subtruncate in the median part of the dorsal and ventral regions, and flattened at the base. Generally the mantle is comparatively thick, but in one of Boschma's specimens the mantle is much thinner and somewhat transparent, dimly revealing the internal septa. The external sac is smooth save for a few irregular grooves and a medial indentation on the surface appressed against the abdomen of the host. The stalk is short and wide and may be surrounded by a thicker layer of chitin. The external cuticle of the mantle is smooth but with some parts more or less wrinkled, the thickness ranging from 12 to 20 microns. The surface of the cuticle, which does not possess excrescences, is divided into interdigital plates, their greater diameter varying from 10 to 15 microns (Pl. 24, fig. 2). No retinacula was seen on the internal cuticle. The male genital organs were found in the posterior part of the body, outside the visceral mass. The testes are of fairly large size and remain completely separated for the whole of their extent. The young of *Ptychas-*

cus glaber leave the egg-membranes and hatch directly into the cypris stage (Pl. 24, fig. 3). The dimensions of one specimen of the parasite, attached to the crab *Sesarma (Holometopus) benedicti*, breadth 7 mm, height 3.5 mm, thickness 2 mm. The largest specimen, attached to *Aratus pisonii*, is 12 mm, breadth, 7 mm, height, and 3.5 mm in thickness.

The hosts of *Ptychascus glaber* are the grapsoid crabs *Sesarma (Holometopus) benedicti* Rathbun and *Aratus pisonii* (A. Milne Edwards). These two crabs live near fresh, brackish, and salt water. *Aratus pisonii* is found on mangroves or along shore on rocks, piles, bushes, and wharves (Rathbun, 1918, p. 323).

Type locality.—The type locality of *Ptychascus glaber* Boschma is Ilha do Marajó, a large island in Brazil, at the mouth of the Amazon River. It was collected in 1923, with two specimens of the parasite attached to the crab *Sesarma (Holometopus) benedicti* Rathbun, and four specimens attached to the mangrove or tree crab *Aratus pisonii* (A. Milne Edwards).

In 1967, Boschma reported *Ptychascus glaber* from the Marianne River, Blanchisseuse Bay, Trinidad, attached to the grapsoid crab *Sesarma (Holometopus) ? miersii* Rathbun. This crab has also been found in the Bahama Islands, Cuba (Isla de Pinos), Jamaica (Montego River), Swan Island in the Caribbean Sea, and in Brazil as far south as Florianópolis (27°35'S, 48°31'W).

To my knowledge *Ptychascus glaber* has not been reported from Florida waters. However, it probably will be found in them, judging from the range of the host crabs *S. benedicti* and *A. pisonii*, the former occurring at Key West, Florida, British Guiana, and Brazil, the latter occurring in numerous localities of Florida, in the Caribbean Sea, in the Western Atlantic to southern Brazil, and in the Eastern Pacific from Peru to Mexico.

Family **LERNAEODISCIDAE** Boschma, 1928, p. 17

Lernaeodiscus bilobatus Boschma

Pl. 21, fig. 4

Lernaeodiscus bilobatus Boschma, 1925, pp. 13, 14, pl. 2, figs. 4, 11, 12.

Lernaeodiscus bilobatus was found attached to the abdomen of *Petrolisthes amoenus* (Guerin), with the axis of the parasite having the same direction as that of the host. The body of *L. bilobatus* is flattish, bilaterally symmetrical, and provided with two lateral pro-

trusions projecting behind the peduncle. The mantle opening is comparatively wide, the surrounding sphincter only slightly developed. The mantle opening lies at the top of a small papilla which is directed toward the extremity of the host. Adjoining the papilla there is a pair of notches dividing the upper surface there into two lobes. The greatest breadth of the type species is 4.5 mm, the height 2.5 mm, and the thickness 1.25 mm.

Type locality. — Caracasbaai, Curaçao, in the Netherlands Antilles.

Lernaeodiscus bilobatus occurs on a single specimen of host (female) at one locality — Caracasbaai — and has not been reported from Florida. It is included in this work, however, because it may eventually be found in Florida waters. According to Schmitt (1935, p. 186), the host crab *Petrolisthes amoenus* occurs in Cuba, Puerto Rico, and Barbados, in addition to Curaçao.

***Lernaeodiscus crenatus* Boschma**

Pl. 25, figs. 5, 6

Lernaeodiscus porcellanae Boschma [not of Müller], 1931, pp. 297, 374-378, figs. 54a-c, 55a, b, 56; 1969a, pp. 417-419.

Lernaeodiscus crenuatus Boschma, 1969a, pp. 417-419.

This parasite from Tobago was originally described by Boschma in 1931 under the name of *Lernaeodiscus porcellanae* Müller. However, in his 1969 paper Boschma observed that although the size, shape, and position of the internal organs corresponded with those of *L. porcellanae*, the lappets of the mantle were of an entirely different appearance. "Whereas in Müller's specimens and in those from La Jolla the lappets remain separated for the whole of their length, while their length exceeds the breadth, the lappets of the Tobago specimen are strongly united sideways, forming a row of very regularly arranged crenatures along the border of the mantle, which are broader than long. This seems to warrant the conclusion that the specimen from Tobago is specifically distinct from *Lernaeodiscus porcellanae*. As it cannot be identified with any of the described species it must be regarded as new. . ."

The body of *Lernaeodiscus crenatus* Boschma which is compressed dorso-ventrally, is bilaterally symmetrical, a structure reflected within by the exactly symmetrical testes which are arranged on each side of the plane dividing the animal in congruent halves. The stalk is small and situated in the center of the posterior region.

Surrounding the stalk there is a thicker chitinous covering than in other parts of the mantle. The external cuticle is approximately 8 microns in thickness, and has a smooth surface. The mantle opening lies within a narrow cleft in the middle of the anterior part of the body, and is directed toward the thorax of the host. Around the margin of the mantle there are a number of lobelike lappets, broader than high, which are more or less symmetrically arranged at the left and right sides. At the ventral surface there is also a concentric row of rounded lobes a short distance in from the margin. The measurements of the type specimen from Tobago are 10.5 mm in breadth, 6.5 mm in height, and 4 mm in thickness.

Type locality.—Tobago, British West Indies. Attached to *Petrolisthes marginatus* Stimpson, an anomuran crab collected April 1916 on a coral reef.

The parasite *Lernaeodiscus crenatus* has not been reported from Florida, and the only localities I have seen listed for the host *Petrolisthes marginatus* in the Caribbean are Puerto Rico, Curaçao, Barbados, and Tobago. The crab *Petrolisthes marginatus* also occurs in the Eastern Pacific (Haig, 1960, pp. 47, 50, 346) from Bahía de Guaymas, Mexico, south to Santa Elena, Ecuador, at depths ranging from shore to 22 fathoms, and often associated with madreporarian corals. Intermediate localities off Mexico are Las Tres Marías, Revilla Gigedo, and Clipperton Islands; off the west coast of Costa Rica; Panama (Islas de Perlas, Isla de Rey, Isla Flamenco, Isla Contadora, Isla Saboga, and Guayabo Chiquito); Colombia (Bahía Humboldt, Bahía Utría); Ecuador (Isla La Plata, 1°18'S, 81°05'W), and the Galápagos Islands.

***Lernaeodiscus porcellanae* Müller**

Pl. 25, figs. 1-3

Lernaeodiscus porcellanae Müller, 1862, pp. 2-5, pl. 1, figs. 1-4; Weltner, 1897b, p. 235; Smith, 1906, pp. 114, 115; van Baal, 1937, pp. 51, 52, 55, 79; Reinhard, 1950a, pp. 126-130, figs. 1A-E; Boschma, 1958, pp. 34, 35; 1969, pp. 413-419, figs. 1-3.

Not *Lernaeodiscus porcellanae* Müller, Boschma = *Lernaeodiscus crenatus* Boschma, *vide* Boschma, 1969, p. 417-419.

As summarized by Boschma, the type of Müller's *Lernaeodiscus porcellanae* is disk-shaped and symmetrical, with the mantle opening and stalk opposite each other in the median plane. There are five to seven lappets at each side of the body, generally with broadened

summits and incised in the middle. At the ventral surface there is often a row of small papillae, next to the border of the visceral mass. The testes are in a symmetrical position, to the right and left of the ventral mesentery. The breadth of the type is slightly over 10 mm.

The holotype of *L. porcellanae* was found in Brazilian waters on the host crab *Petrolisthes galathinus* (Bosc). In the United States, the parasite has been found on the east coast in North Carolina, attached to *Petrolisthes galathinus*, and on the west coast at La Jolla, California, attached to the host crab *Petrolisthes eriomerus* Stimpson.

The rhizocephalid *Lernaeodiscus porcellanae* from North Carolina was described by Reinhard as being nearly symmetrical, with numerous subregular lappets on the margin of the dorsal surface and with irregular lappets on the margin of the ventral surface, the latter a little below the former. The body is bilobar, the lobes formed by the deep concavity of the posterior, in which the stalk is situated. The stalk is short and narrow, and is concentrically wrinkled. The chitinous flange at the base of the stalk is composed of a substance different from that of the external cuticle. The external cuticle of the mantle is smooth and varies in thickness from 7 to 14 microns, and there are no excrescences on the surface. The internal cuticle lacks retinacula. The mantle opening, which is situated opposite the stalk, is small and subcircular, and is surrounded by a low boss containing the spinter and marked by a number of radii. The specimens of *L. porcellanae* described by Reinhard from North Carolina range from 5 mm in breadth, 3 mm in length, and 2 mm in thickness to 11 mm $\times$ 6 mm $\times$ 4 mm. The lappets are more numerous in smaller specimens than in the larger.

The rhizocephalid *Lernaeodiscus porcellanae* from La Jolla, California, is described by Boschma as being somewhat asymmetrical, with slender lappets on the margin of the dorsal surface. On the larger of the two specimens collected, the lappets on the dorsal surface lie farther down from the margin of the dorsal surface than do those on the North Carolina specimens; on the smaller of the two California specimens lappets are not even present. The body is only slightly bilobar at the posterior. The stalk within the concavity is short, and oval in outline. The external cuticle of the mantle is very thin, not over 3 microns. The internal cuticle is also extremely thin.

The mantle opening at the top of a small protuberance lies at some distance from the anterior margin and is not found exactly in the median plane. The smallest of the two specimens of *L. porcellanae* examined by Boschma from La Jolla was 4.1 mm in breadth, 2.9 mm in length, and about 1 mm in thickness; the larger was 7.5 mm $\times$ 6.8 mm $\times$ nearly 2 mm. The host was *Petrolisthes eriomereus* Stimpson.

Type locality. — Coast of Brazil (Müller).

Other localities. — Black Rocks, off New River, North Carolina, on *Petrolisthes galathinus* (Bosc). Also in North Carolina in New River Inlet, 6-7 fathoms, and mouth of Fear River, obtained by the "Fish-Hawk." La Jolla, California, on *Petrolisthes eriomereus* Stimpson.

I have not seen a report of the parasite *L. porcellanae* having been found in Florida waters, but it undoubtedly is present, since the host crab *Petrolisthes galathinus* occurs in abundance in the Gulf of Mexico, 8 miles south of Alligator Point, Franklin Co., Florida, according to L. G. Abele of Florida State University (1970, p. 43). Abele stated also that *Petrolisthes galathinus* ranges from North Carolina through the Gulf of Mexico and the Caribbean Sea to Ilha da Trindade, Brazil, and in the Eastern Pacific from off Ecuador, Panama, and Costa Rica.

***Lernaeodiscus schmitti* Reinhard**

Pl. 25, fig. 4

Lernaeodiscus schmitti Reinhard, 1950a, pp. 130, 131, figs. 2A-C.

The following notes are taken from Reinhard's excellent original description.

The parasite *Lernaeodiscus schmitti* was attached to the second abdominal segment of the host, *Munida iris* A. Milne Edwards. The external form of *L. schmitti* is bilaterally symmetrical, flattened dorso-ventrally, and bears large winglike lateral lobes without lapets. The antero-posterior axis is short in proportion to the breadth of the animal, and is a diagnostic character serving to differentiate this species from others of the genus *Lernaeodiscus*. The mantle opening and stalk are in the median plane, the former at the anterior extremity, the latter at some distance from the posterior margin. The mantle opening is round, and has well-developed sphincter muscles around it, although the musculature of the mantle proper

is not prominent. The stalk, which is subterminal on the dorsal surface, is somewhat prolonged and covered with chiton much thicker than that of the rest of the mantle; however, the stalk is without internal chitinous projections. The holotype of *L. schmitti* measures 4 mm in length (antero-posterior axis), 17 mm in breadth, and 3 mm in thickness (dorso-ventral) at the midline to 5 mm at the expanded portion of the lateral lobes.

Type locality. — A single specimen of the host *Munida iris* was collected off Tortugas, Florida, in 135-156 fathoms, by Dr. Waldo L. Schmitt, July 2, 1936.

Although Reinhard's citation above is the only one I have been able to find, it is likely that additional specimens of *Lernaeodiscus schmitti* will be found in waters surrounding the Tortugas.

Suborder **AKENTROGONIDA** Häfele, 1911

Family **UNCERTAIN**

Genus **THOMPSONIA**, Kossman, 1873, p. 132

Thompsonia cubensis Reinhard and Stewart

Pl. 27, fig. 15

Thompsonia cubensis Reinhard and Stewart, 1956, pp. 162-168, figs. 1-7.

The following remarks are from the work of Reinhard and Stewart.

The parasite *Thompsonia cubensis* occurs on the anomuran crab *Munida stimpsoni* A. Milne Edwards to which it is attached on the underside of the abdomen and thorax, and the basal portions of the abdominal and thoracic appendages. On one specimen of crab, the parasites were found on the maxillipeds and sides of the rostrum. The external sac is globular when small (Pl. 27, fig. 15) but becomes ovoid with growth, the size ranging from 0.2 to 2.0 mm in length and 0.4 to 1.5 mm in width. Mature sacs average 1.4 mm in length and 1.1 mm in width. The length of the stalk at any stage is one-sixth to one-seventh the length of the sac, with an average length in adult specimens of 0.24 mm. The nonmuscular mantle consists of an external and internal cuticle formed respectively by an outer and inner epithelium. The testes originate alongside the apical pole. Later they lie embedded in the surface of the ovary where they reach their full development at the time they are ready for fertilization. The eggs are fertilized *in situ*, and reproduction is hermaphroditic, the larvae

being liberated in the cypris stage. A birth pore is absent. Subsequently the testes degenerate.

Type locality.—The type locality of *Thompsonia cubensis* is the Old Bahama Channel off Punta Alegre (about 22°45'N, 78°8'W), on the north coast of Cuba, and Cayo Coco, northeast of Punta Alegre, off the north coast of Cuba, about 250 statute miles south of Miami, Florida. All specimens were recovered by the Atlantis Expedition to the West Indies: four of the host *Munida stimpsoni* on March 1, 1938, with 139 parasites, MCZ Nos. 11478 and 11479 at depths of 150 to 180 fathoms, and two hosts on April 29, 1939, with 108 parasites, MCZ Nos. 11483 and 11484, at depths of 200 to 230 fathoms. The specimens off Cayo Coco (MCZ Nos. 11485 and 11486) were obtained at depths of 225 and 180 fathoms, respectively.

Other localities.—The host of the parasite *Thompsonia cubensis* is *Munida stimpsoni*, the latter recorded from as far north as 23°32'N, 83°14'W (northwest coast of Cuba) and as far south as off Recife (8°06'S, 34°53'W) Brazil. *M. stimpsoni* is a common species in the Caribbean Sea, particularly in the waters off Puerto Rico. According to Schmitt (1935, p. 178), the type locality of *Munida stimpsoni* is at "Blake" sta. 143 (17°31'N, 69°43'30"W), south off Ciudad Trujillo, Dominican Republic. It is otherwise well distributed through the Greater and Lesser Antilles, including St. Thomas and St. Croix, at depths of 73 to 1105 fathoms.

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PLATES

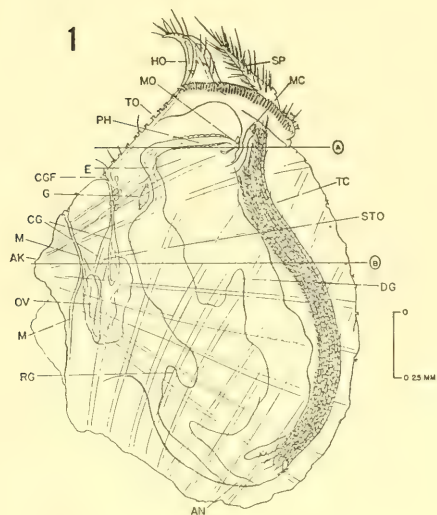
EXPLANATION OF PLATE 20

All figures on this plate reduced 1/2 from originals.

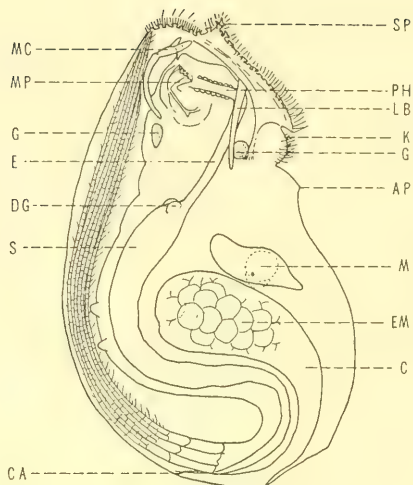
Figure	Page
1. Lithoglyptes spinatus Tomlinson and Newman	174
Drawing of female holotype from Tomlinson and Newman, 1960, p. 520.	
Legend: AK, attachment knob; AN, anus; ANT, antennule; BS, blood sinus; CG, cement gland; CGF, cement gland furrow; DG, digestive gland; E, esophagus; G, ganglion; HO, hook; M, muscle; MC, mouth cirrus; MO, mouth; MP, mouth parts; OV, ovary; PH, pharynx; RG, rectal gland; RS, renal space; SP, spine; TC, terminal cirri; TO, tooth. True scale shown by marker.	
2, 3. Kochlorine floridana H. W. Wells and Tomlinson	176
Drawing of female from Wells and Tomlinson, 1966, p. 29.	
2. Legend: AP, attachment process; C, mantle cavity; CA, caudal appendage; DG, digestive glands; E, esophagus; EM, embryos; G, ganglion; K, knob; LB, lateral bar; M, male; MC, mouth cirrus; PH, pharynx; S, stomach; SP, spine.	
Drawing of specimen from Puerto Rico, after Tomlinson, 1969a, p. 74.	
3. Letters <i>a</i> to <i>f</i> refer to <i>a</i> in legend. Legend: <i>a</i> , female with males, side view; <i>b</i> , opercular details; <i>c</i> , mouth area showing mouth cirrus smaller ramus and lateral bristles on inside of anterior ramus, the mouth cirrus faintly plumose; <i>d</i> , mandible; <i>e</i> , first maxilla; <i>f</i> , posterior thorax, base of terminal cirri, and caudal appendage; <i>g</i> , mature male; <i>h</i> , cyprid larva; <i>i</i> , burrow aperture in coral rock from Puerto Rico. Comparative scales as shown.	
4, 5. Trypetesa lampas (Hancock)	179
Reproduction of Hancock's plate VIII, 1849.	
4. Explanation of pl. VIII. 4-1. Portion of <i>Fusus antiquus</i> exhibiting numerous specimens of <i>Alcippe lampas</i> in the columella and sides of whorls; <i>a</i> , stain caused by <i>A. lampas</i> ; <i>b</i> , slit by which it communicates with the water. 4-2. Much enlarged view of the external appearance of the chamber of <i>A. lampas</i> ; <i>a</i> , stain seen through the shell, exhibiting pale radiating lines and punctures; <i>b</i> , slit; <i>c</i> , calcareous layer partially filling the chamber, and projecting beyond the margins of the slit; <i>d</i> , calcareous granules filling up posterior extremity of chamber. 4-3. Upper view of <i>A. lampas</i> removed from its chamber. <i>a</i> , anterior portion containing the arms and true body; <i>b</i> , broad disclike portion corresponding to the pedicle of the pedunculate barnacles; <i>c</i> , valvular lips; <i>c'</i> , slit; <i>d</i> , posterior terminal points of lips; <i>e</i> , horny plate; <i>f</i> , arms partially exerted; <i>g</i> , the point at which the animal is attached to the chamber. 4-4, 4-5. Under and side views of <i>A. lampas</i> ; letters as in 4-3. 4-6. Anterior portion laid open to show true body and arms. <i>a</i> , one of the valvular lips; <i>b</i> , the other valvular lip cut across and laid back; <i>c</i> , fleshy pedi-	

Explanation of Plate 20 continued on page 217

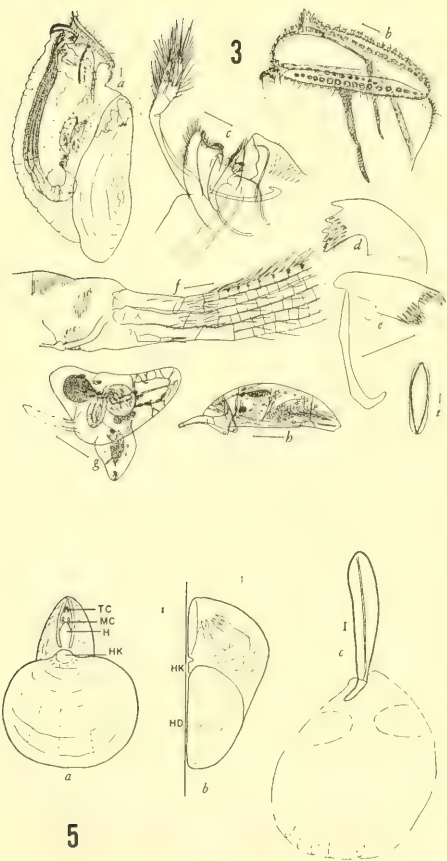
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EXPLANATION OF PLATE 20 continued

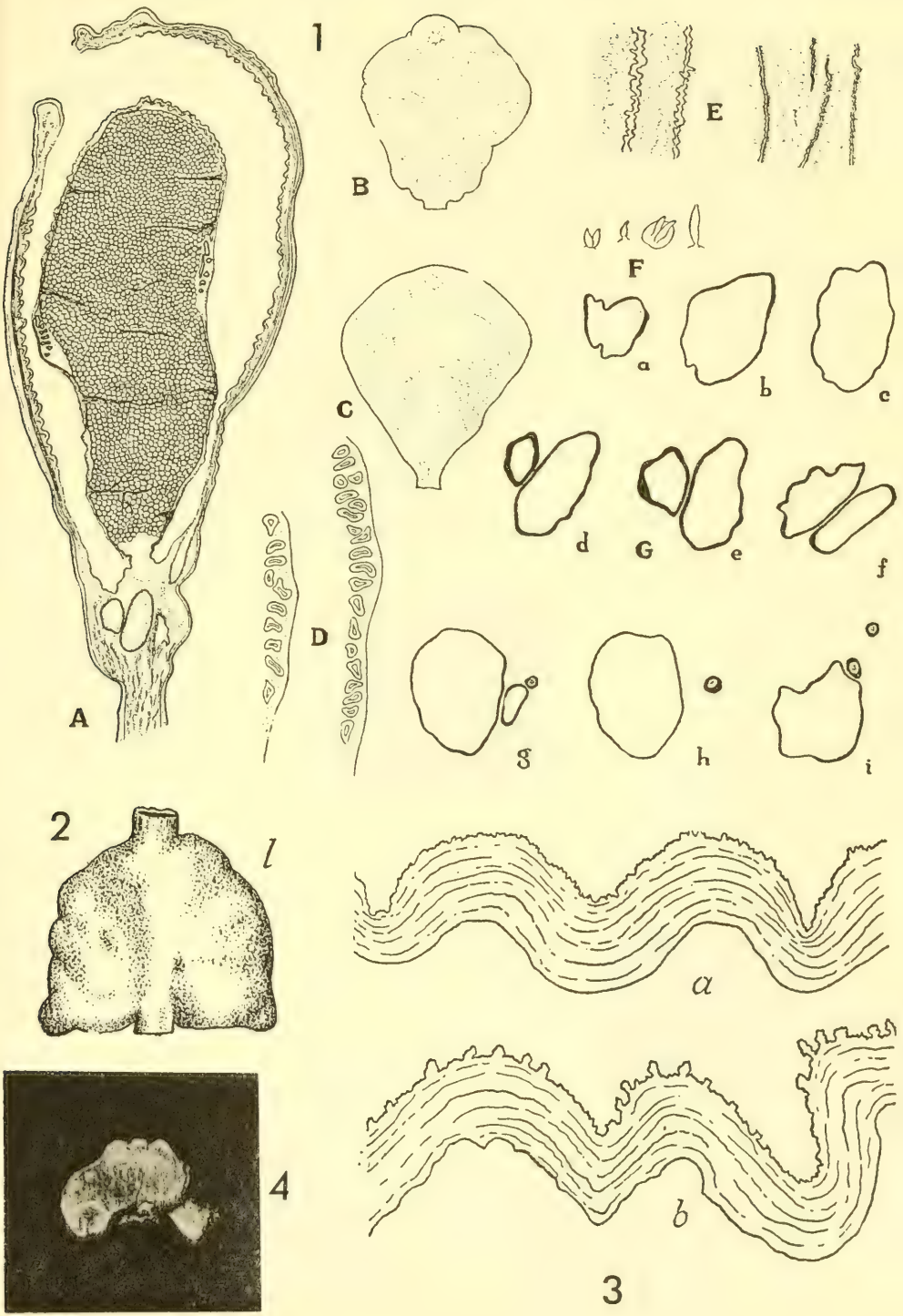
cle supporting the arms *d*; *e*, mouth; *f*, upper lip; *g*, rostrated termination of upper lip; *h*, arms or palpi by the sides of the mouth furnished with pincers; *i*, branchiae. 4-7. Portion of the true body as seen in the compressor. *a*, upper lip; *b*, rostrated portion of upper lip; *d*, arms or palps by sides of mouth; *e*, prehensile arms; *e'*, mouth; *f*, the outer or first pair of mandibles; *g*, second pair of mandibles; *h*, third or innermost pair of mandibles; *i*, branchiae. 4-8. A few of the plates or setae of the branchiae highly magnified, exhibiting a double channel at the broad extremity which is bifid. 4-9. Prehensile cushion of the arms.

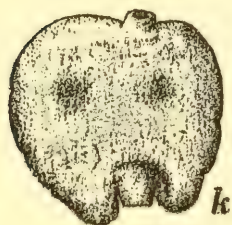
From Tomlinson 1969a, p. 128.

5. *Trypetesa lampas* on *Lunatia heros* from Falmouth, Massachusetts. Abbreviations: TC, thoracic cirri; MC, mouth cirrus; H, head; HK, horny knob; HD, horny disk; *a*, female viewed perpendicular to shell surface; *b*, viewed parallel to shell surface; *c*, female in burrow, surface view. Comparative scales shown by markers.

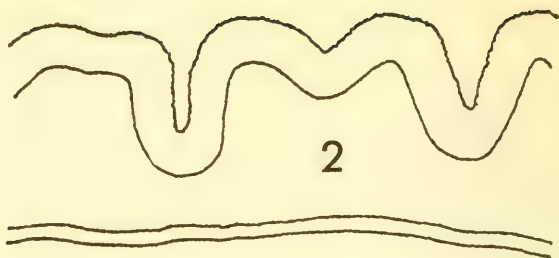
EXPLANATION OF PLATE 21

Figure	Page
1. Sacculina americana Reinhard	185
Illustrations and legend from Reinhard, 1955, p. 76.	
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From Boschma, 1925, pl. II, fig. 4.	
External view of sac, $\times 5$. Holotype.	





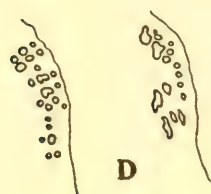
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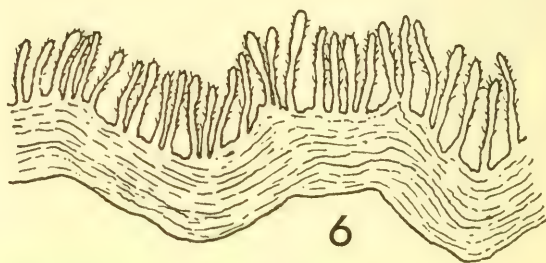
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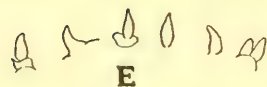
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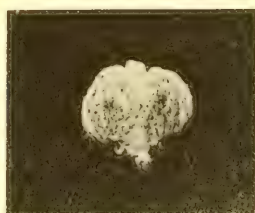
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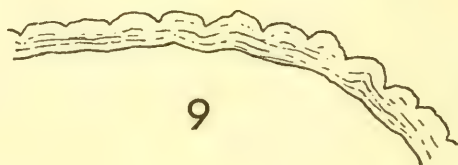
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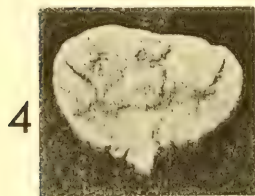


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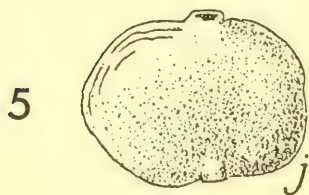
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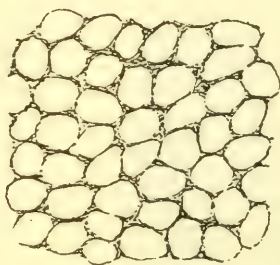
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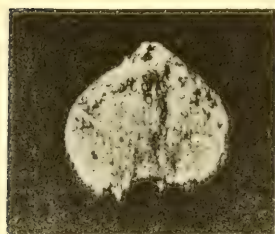
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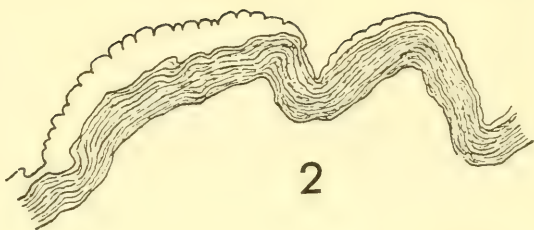
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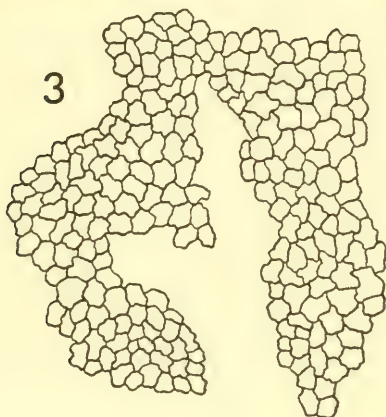
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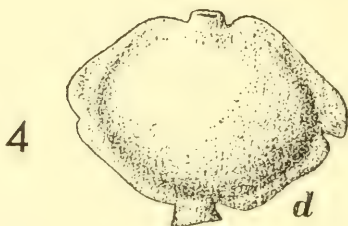
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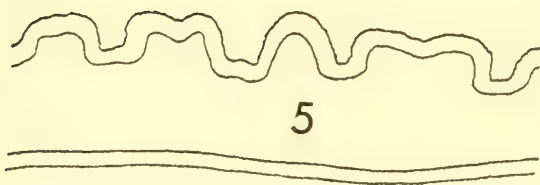
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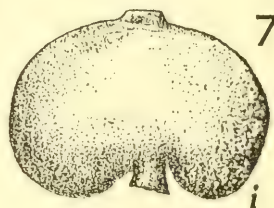


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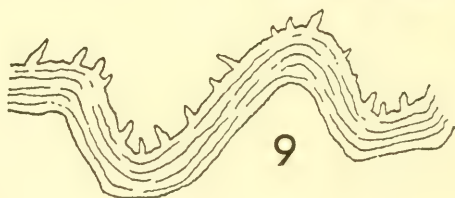


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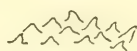
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A



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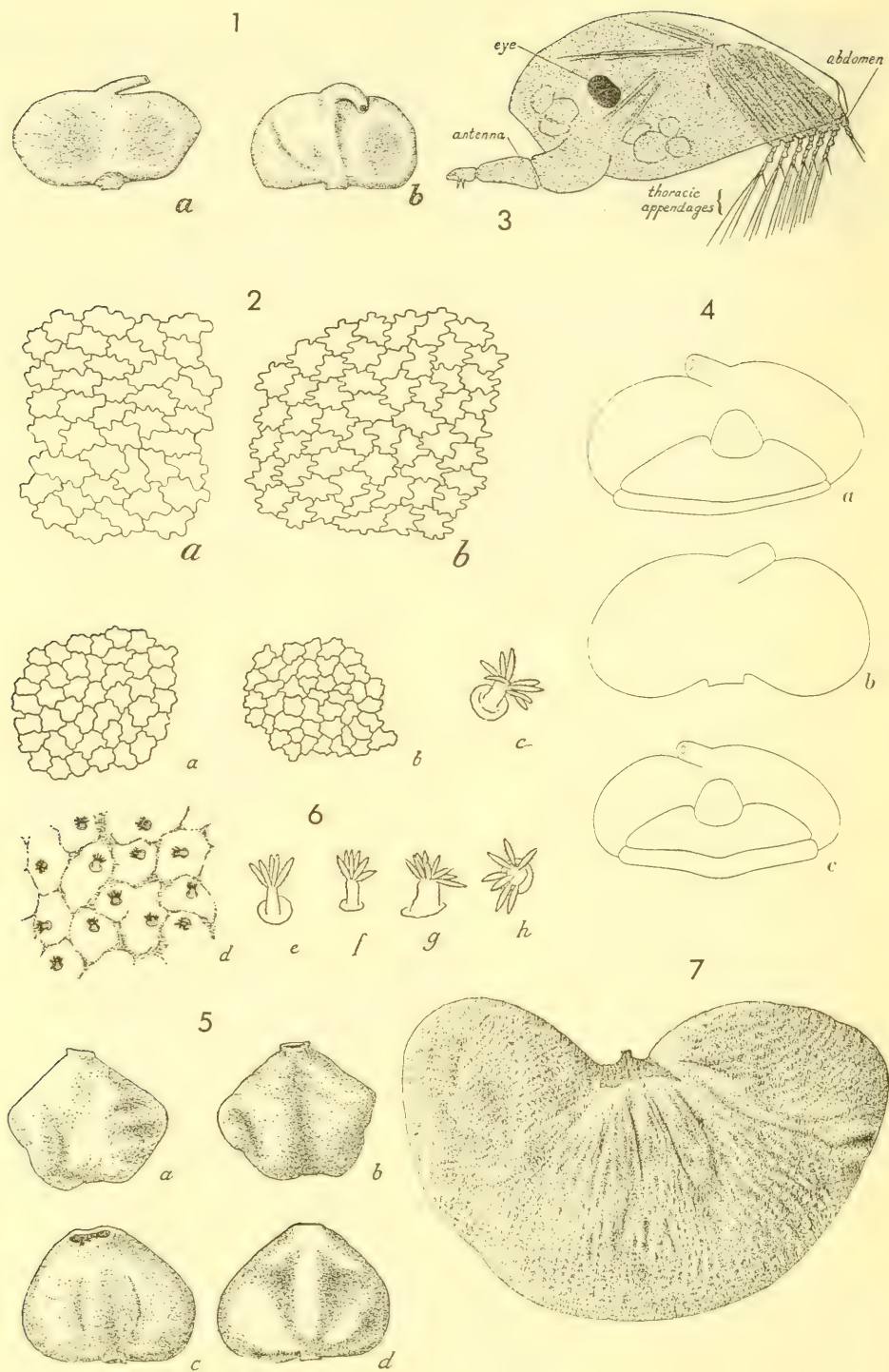


C

8



D



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All figures on this plate reduced 1/4 from originals.

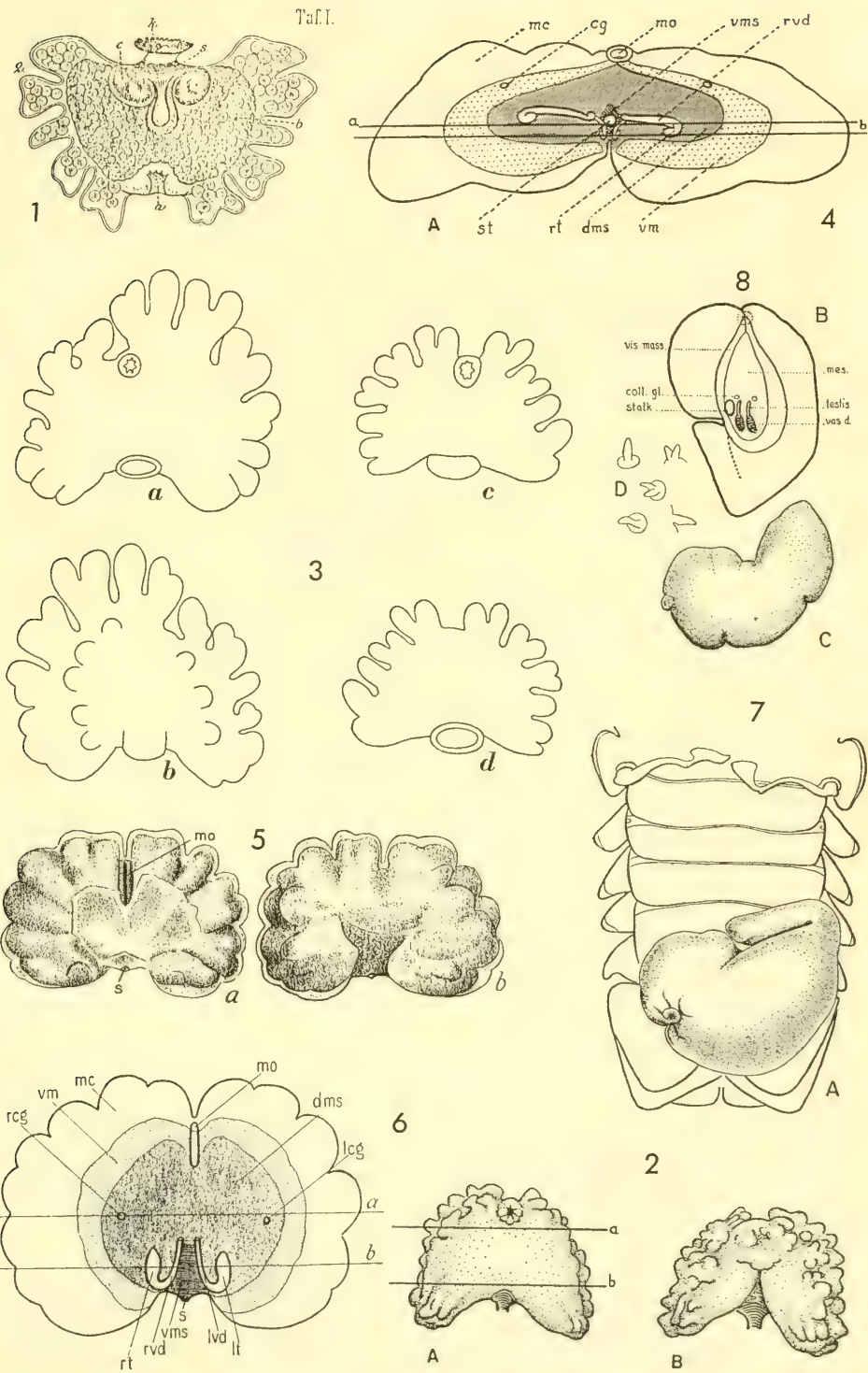
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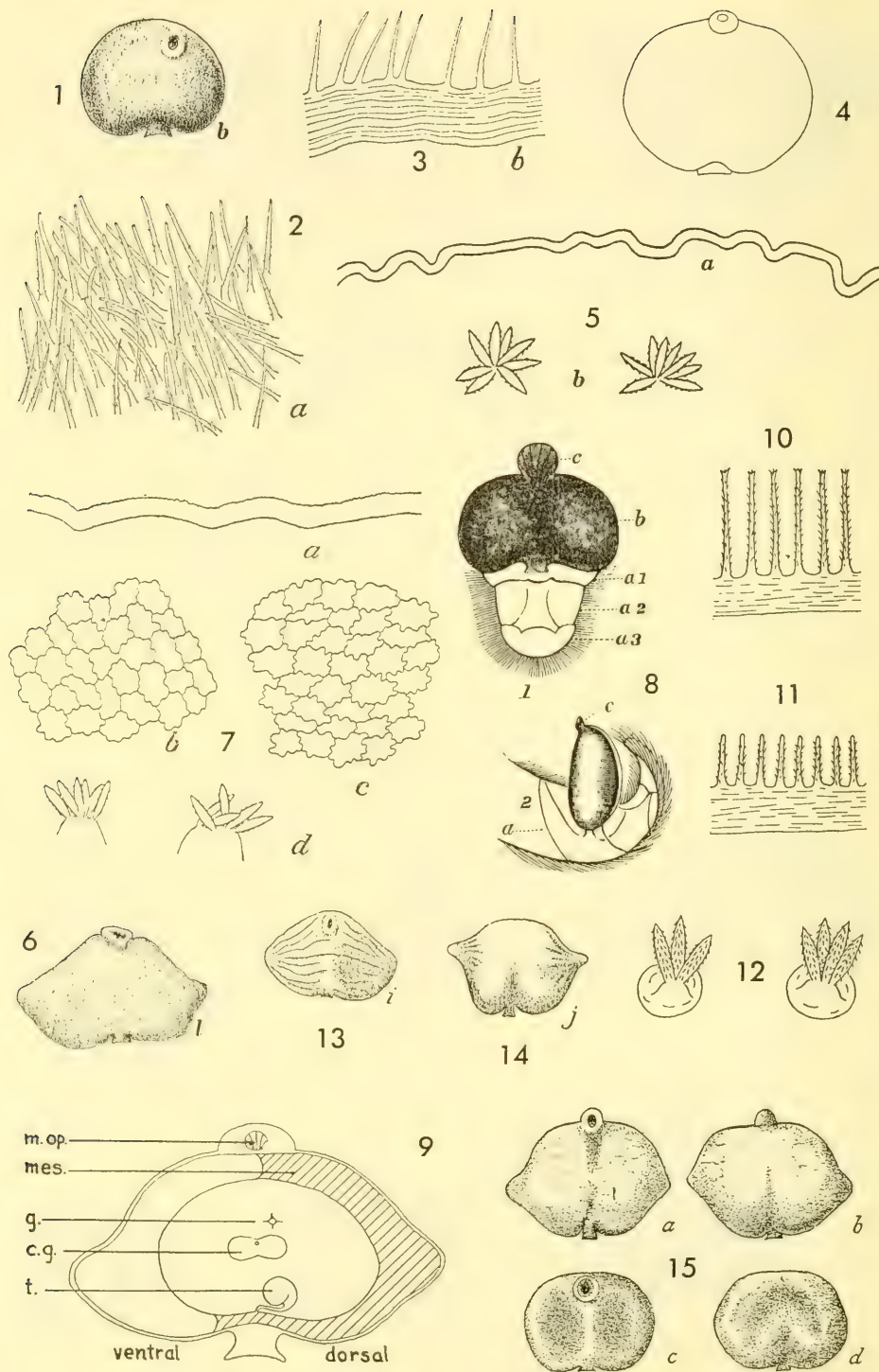
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Taf. I.





EXPLANATION OF PLATE 26

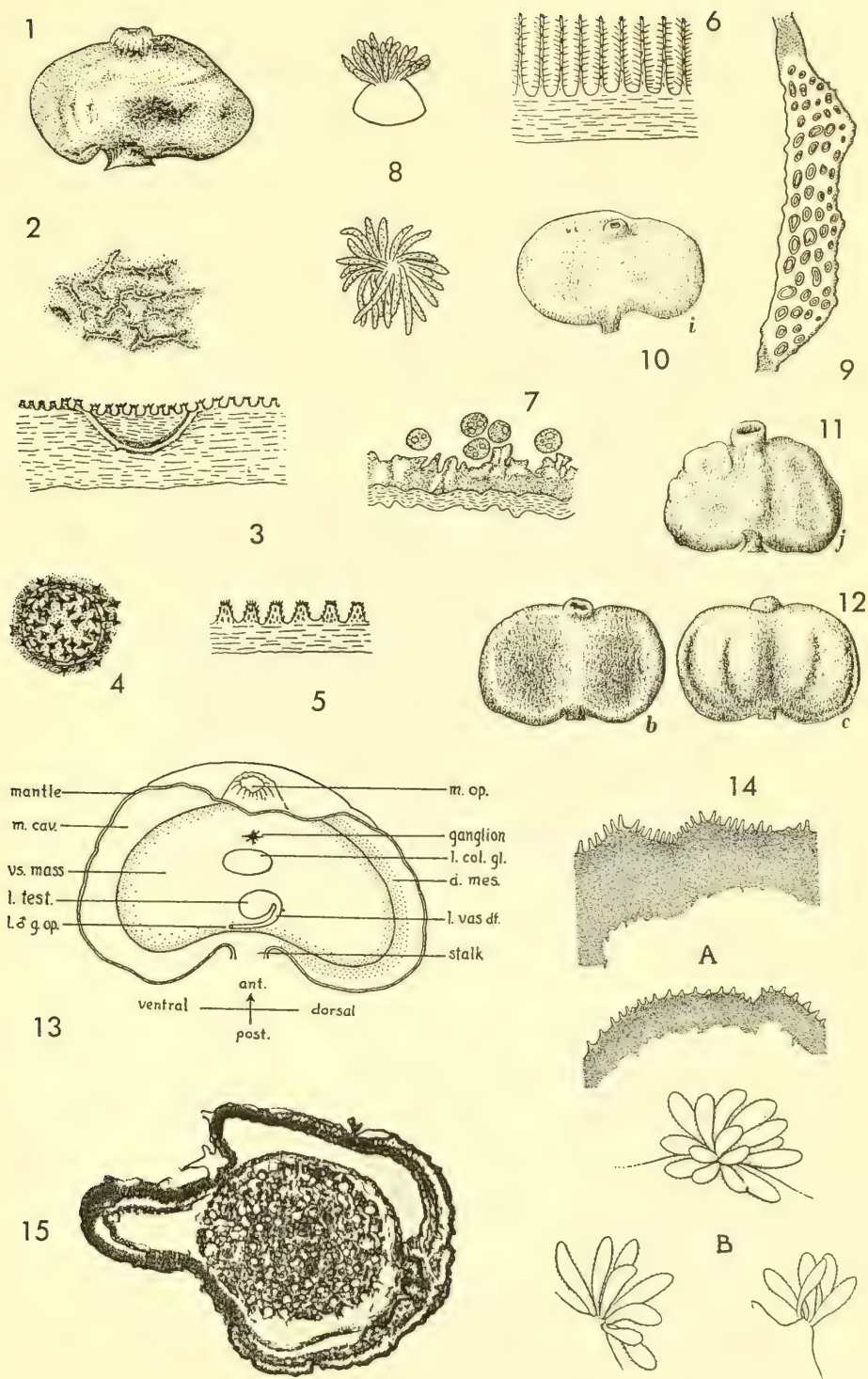
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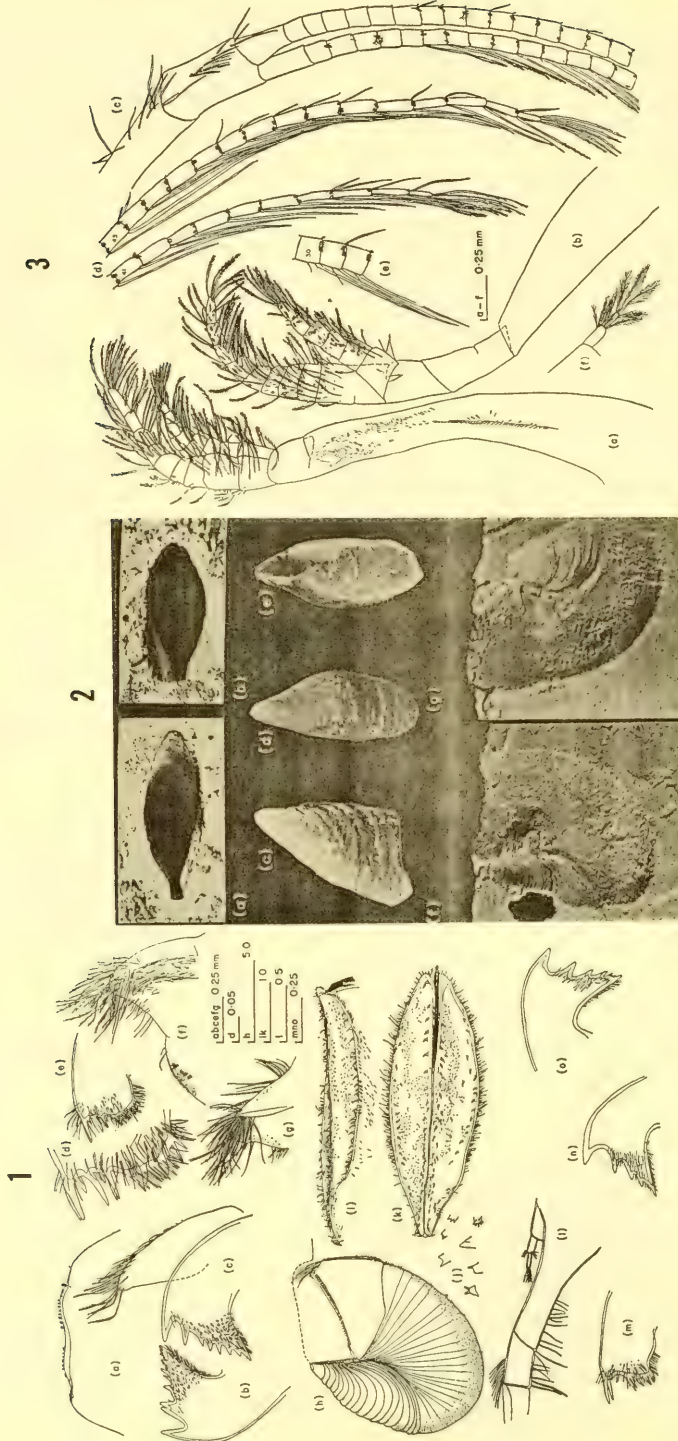
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